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ADAPTIVE GENE SUBSTITUTIONS IN TASMANIAN EUCALYPTS: I. GENES CONTROLLING THE DEVELOPMENT OF GLAUCOUSNESS

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INTRODUCTION

The question of the adaptive value of the morphological characteristics, which the taxonomist uses to separate species populations, is still one of the crucial problems of evolutionary biology. Such diagnostic characteristics are selected by the taxonomist because of their constancy within, and discontinuity between, species populations. The museum or herbarium taxonomist, if he thinks at all on such general problems, is usually content to adopt the views put forward by Robson and Richards (1936) that the diagnostic characters have no selective value. If, on the other hand, we consider the problem from the point of view of the genetical theory of evolution, four answers to the question are possible.

(1) The diagnostic characteristics are the result of the action of genes which have become fixed by genetic drift early in the history of the species when presumably the total population was small. In this case the characteristics may have no adaptive value.

(2) The diagnostic characteristics are the irrelevant by-products of the activity of important genes, which must, therefore, be constant members of the gene complement of the species population (pleiotropic gene-action).

(3) The diagnostic characteristics are the result of developmental correlations, e.g., allometric growth relationships. If, for example, an increase of size is brought about by selection, any characteristic which is developmentally correlated with size, must also change. If such correlated changes are selectively neutral, they will persist.

(4) The diagnostic characteristics have, or had during the past history of the species, some selective value and were brought into being by the action of natural selection on adaptively random gene mutation and recombination.

As Stebbins (1950) has emphasized, it is at present impossible to say which mechanism may have been operating in any particular case of evolutionary divergence without a very close study. However, when such close study is carried out, the adaptive value of diagnostic characteristics often becomes apparent, e.g., Lack's (1947) reconsideration of Darwin's finches, the work of Vavilov,

etc., on adaptations to cultivation in both weeds and economic plants.

The genus *Eucalyptus* embraces according to Blakely (1934) 500 species and 138 varieties. Since 1934 approximately 20 new species have been described. Like so many genera of trees all species appear to be diploid ($2 = 22$ is known from over 30 species; Aitken, 1947) and to reproduce sexually. Although the different "species" as described by Blakely and other authors are of very diverse genetic constitution, some being hybrids or segregates from recent hybrids (Brett, 1937; Pryor, 1950, 1952) or simple mutants, others being geographical subspecies, etc., the genus presents great advantages in the study of the adaptive value of diagnostic characteristics. A *Euclayptus* forest is usually made up of several species. For example, seven can occur along a quarter of a mile of road in Tasmania. In the forests is developed a complex mosaic of species, the different species tending to have slightly different ecological requirements. Where the ecological conditions show a gradient as in ascending a mountain, the different species replace each other along the gradient, the forest at any one point usually showing the presence of three or four species. Among the Tasmanian species *regnans* is the only one which often forms extensive pure stands.

This paper is an attempt to determine whether any correlations exist between important taxonomic characteristics and ecological habitat. The characteristic chosen is the development of white, waxy bloom (glaucousness) on leaves and stems. It is of great diagnostic importance in the morphological definition of species in numerous groups of eucalypts. Blakely attempted to use it in the definition of several of his series. e.g., the Globulares and the Viminales, a procedure which, however, leads to the taxonomic separation of closely related species.

In what follows the nomenclature will be based on that of Blakely (1934). Blakely's "Key" is the latest attempt at a taxonomic treatment of the genus as a whole. I can see no point in attempting to follow the changes of names which our nomenclaturists (e.g., Cameron, 1946; Johnson, 1952) are advocating because of a pedantic adherence to the Rules of "Typification," and of Priority. I shall use 1934 as the base date for nomenclature in the genus *Eucalyptus* for reasons which I have given elsewhere (Barber, 1952, 1953). Blakely left 638 suites of specimens to support his definition of the different species and varieties. This seems scientifically a better procedure than attempting to determine the application of a name for a species on the basis of a single "type" specimen. I have also taken the liberty of deleting the abbreviation *E* (= Eucalyptus, L'Heritier, 1788) before the specific names (or epithets) which are italicized throughout.

General Characteristics of Glaucousness

There are two types of bloom present on Tasmanian eucalypts. The first type shows itself in a blue-gray color of the foliage which is stable to the touch. The color is also stable to fat solvents such as petrol-ether, benzene, etc. A drop of such a solvent placed on the leaf rapidly penetrates, the area of penetration momentarily becoming green. As the solvent evaporates the blue-green color reappears. This type of glaucousness I shall refer to as *structural.* It is presumably caused by some structural properties of the epidermis or underlying tissues. It is always present on *gigantea* juvenile (or intermediate) leaves which are blue-gray contrasting with the brilliant green of the related *obliqua* and *regnans.* In *gigantea* the epidermal cells are characteristically dome-shaped, contrasting with the flatter cells of *obliqua* and *regnans. Ovata, salicifolia* and probably *pauciflora* also sometimes show this structural glaucousness (see table 1).

The second type of bloom, which is

TABLE 1. *Eucalypt species in Tasmania*

Species	Waxy glaucousness	M.P. of wax, ° C.	Min. temp. of survival in U. K., ° F.	Altitudinal range in ft. in Tasmania	Remarks
Macrantherae					
aggregata	green	—	10	500–3,000	
ovata	green	—	15	0–2,000	sometimes shows structural glaucousness
subcrenulata	green	—	5–10	1,500–3,500	including *E. johnstoni*
vernicosa	green	—	0–5	2,000–4,500	
viminalis	green	—	15	0–1,500	
gunnii	clinal	59–61	0	2,000–3,500	
urnigera	clinal	59–61	10	2,000–3,500	
"vim-dal"	clinal	?	?	2,000–3,000	widespread, subalpine, intermediate between *dalrympleana* and *viminalis*
cordata	glaucous	57–58	15	500–2,500	
globulus	glaucous	58–59	20	0–1,500	
morrisbyi	glaucous	58–59	?	0–500	known only from 2 localities in S.
perriniana	glaucous	59–60	15	1,000–2,000	known only from 2 localities
rubida	glaucous	60–62	15	1,000–2,500	
Renantherae					
obliqua	green	—	20	0–2,000	
regnans	green	—	15–20	0–2,000	
gigantea	clinal	51–53	10	1,000–3,500	juvenile leaves always show structural glaucousness
pauciflora	clinal	52–54	10	0–3,500	juvenile leaves sometimes show structural glaucousness
sieberiana	clinal?	52–54	20–25	0–2,000	restricted to N.E.
coccifera	clinal	46–47	5	2,000–4,500	juvenile leaves show structural glaucousness
linearis	clinal	?	20–25	500–2,500	
salicifolia	clinal	46–48	15	0–3,000	juvenile leaves sometimes show structural glaucousness
simmondsi	clinal?	?	?	0–1,500	sometimes shows structural glaucousness
tasmanica	clinal?	46–48	20–25	0–1,500	great variation in adult glaucousness
risdoni	glaucous	45–47	20–25	0–500	known only from Risdom Hills

The table omits several "species" which have been listed in Blakeley (1934) for reasons given in Brett (1937) and Barber and Jackson (unpubl.). I have coined the name "vim-dal" to represent the populations of white gum associated with *gigantea*. Phenotypically these populations appear to be intermediate between *dalrympleana* of the Australian mainland and *viminalis*.

It is, perhaps, unfortunate that two temperature scales are employed in this one table but it seems impossible, in the English speaking countries, to obtain agreement between chemists, on the one hand, and foresters and climatologists on the other.

the type we shall be concerned with in this paper, consists of a thick deposit of brilliant white wax. Surface examination under the microscope of leaves or stems shows that the deposit consists either of needle-shaped crystals or it is granular and apparently amorphous. In both cases light rubbing with finger tips may remove the deposit completely, exposing either the green or red (anthocyanin) or yellow tissues beneath. The waxy deposit is easily removed by dipping leaves or stems into petrol-ether or benzene, and can be purified as long crystals. When a drop of these solvents is placed on the leaf or stem the glaucousness does not reappear when the solvent has evaporated, presumably because the

wax is deposited as a smooth layer which does not scatter the light. The waxy deposits have characteristic melting points for the different species or groups of related species. Table 1 gives the melting point determined by floating small pieces of leaf or bark on the surface of a beaker of water and slowly heating. The values so obtained will probably be rather higher than the true melting point. The melting point is usually fairly sharp, and is shown by the leaf rapidly becoming green over a temperature rise of 1–2° C. The glaucousness does not reappear on cooling. Structural glaucousness is more stable towards heat under these conditions, disappearing only when the cells are killed and permeability destroyed.

Table 1 shows that an interesting correlation exists between taxonomy and melting point. The Macrantherae have a wax melting point between 57–61° C. All the Tasmanian species belong to Blakely's series Globulares. In the Renantherae two types of wax exist. In Blakely's series Piperitales the melting point is between 45–48° C., whilst in *gigantea, sieberiana* (series Fraxinales) and *pauciflora* (series Longitudinales) a wax of melting point 51–54° C. is formed.

The waxy glaucousness in many species is unstable tending to fade in the hot summer sun. Whether this is due to melting or sublimation of the crystals is unknown. In *risdoni* this fading is particularly marked. After a single hot day, leaves fully exposed to the sun may have faded while leaves in the shade may still be fully glaucous.

As regards the detailed chemistry of the deposit in different species very little is known. Kreger (1949) has deduced from X-ray powder diagrams that the wax of *globulus* contains as a major constituent a molecule with chain length of C_{33} probably either n-tritriacontane-17-one or -ol.

The distribution of waxy glaucousness during growth of the plant shows characteristic differences of pattern between the different species. There are also considerable variations within the same species. The simplest type is seen in *risdoni, perriniana, cordata,* etc., where glaucousness persists throughout growth. In other cases the heteroblastic juvenile foliage is typically heavily glaucous, but in the adult the glaucousness is either absent altogether or confined to the young leaves, stems and flower buds. It rapidly fades as the adult leaves mature. Examples of this type are *rubida, urnigera* and *gunnii.* In other cases, e.g., *globulus,* the juvenile foliage is heavily glaucous but in the adult glaucousness is restricted to the flower buds and young fruit. Another pattern is shown by *gigantea* where waxy glaucousness is restricted to the young stems and flower buds, the leaves having structural glaucousness only. The most complex pattern of glaucousness is found in *coccifera.* In this species the typical pattern is as follows: the juvenile foliage, consisting of opposite and broad-elliptical leaves, has structural glaucousness. The juvenile stems are heavily glandular-hairy without a trace of glaucousness. The intermediate foliage formed during the transition to adult type of foliage is usually heavily waxy-glaucous on both leaves and stems. In the adult tree waxy glaucousness may persist particularly on the stems but often it is a transient phenomenon as in *rubida* or it is restricted to the flower buds and young fruit as in *globulus.*

The development of the wax is also dependent on growth conditions. Cold temperatures seem to promote the development of the wax where the genotype allows it. For example, *risdoni* grown in a heated glasshouse during the winter remains nearly green. Plants outside experiencing mild frost become heavily glaucous. Kurtz (1951) has shown that the degree of development of wax in Nicotiana is also influenced by degree of available soil moisture, drought tending to increase the amount of cuticular wax. It is unknown whether this effect holds for Eucalyptus as well.

Types of Variation of Glaucousness

Table 1 gives a rough classification of Tasmanian eucalypts according to degree and variability of glaucousness, frost resistance and altitudinal range in Tasmania. The figures for frost resistance are derived from Martin's observations (1948 and unpub.).

The classification of the 24 Tasmanian species into the three groups as regards waxy glaucousness is based on a preliminary field survey. The survey has shown that variation in glaucousness follows two patterns. A single species may show both patterns or only one or neither pattern. The two patterns are best exemplified by *salicifolia*. In some parts of its range, e.g., Risdon Hill across the river from Hobart, some individual trees may be distinctly glaucous. These trees are almost certainly the result of recent hybridization between *risdoni* and *salicifolia*. A hybrid swarm connects these two species in this locality and seed from trees intermediate in phenotype segregates a range of types showing the various character combinations possible between the broad, glaucous, opposite, juvenile foliage of *risdoni* and the narrow, green, alternate juveniles of *salicifolia*. Green *risdoni* trees are also a rare constituent of the forest (Barber and Paton unpubl.). The F_1 hybrid has been successfully made by Brett and Gilbert (unpubl.). Such sporadic variations occur in several species. Another example is *globulus* which occasionally shows variants with green juvenile foliage. McAulay (1937) has shown that *globulus* will hybridize with *ovata* (green). Segregation from rare interspecific hybridization is, thus, one possible explanation of the rare green variants. In other cases, they might have arisen by recent mutation. However, whatever its origin, such sporadic and rare variation in glaucousness has no ecological significance under present-day conditions. It is the result of chance hybridization and segregation or chance mutation.

The other pattern of variation is well exemplified by the behavior of *salicifolia* on ascending from Mathinna at about 1,000 feet altitude to Mathinna Plains at 2,500 feet in the N.E. mountains of Tasmania. In the river valley, the *salicifolia* population is green. At 1,800 feet occasional waxy glaucous plants appear. At 2,500 feet which is close to altitude limit of the species in this area, the population is predominantly (over 90 per cent) glaucous. Thus, this type of variation is clinal. It regularity, as we shall see later, means that the development of glaucousness must have some adaptive significance. In the table it is this clinal variation in degree of glaucousness which is considered. The rare sporadic type is ignored.

Of the 24 species listed in table 1, seven are wholly green, six wholly glaucous while eight show clinal variations in degree of glaucousness. The remaining three species are also probably clinal but analysis is not complete. The table also shows that there is no apparent correlation between the degree of glaucousness of a species and either frost resistance (in U. K.) or altitudinal range in Tasmania. Of the three most frost-resistant types, *vernicosa* is wholly green while *gunnii* and *coccifera* are clinally varying species.

Clinal Variation of Glaucousness Within the Species

Fig. 1 is an attempt to show the types of clinal variation within the species *gigantea, gunnii* and *coccifera*. It gives a diagram of part of the succession of the eucalypts found on ascending from Golden Valley at 1,200 feet to Great Lake at 3,400 feet in the Central North of Tasmania. The transect shows two types of cline which have been observed in the clinal species. The simplest cline is shown in *coccifera* where the trees growing at the lowest elevations on the north slope have no waxy glaucousness. As exposure increases a rapid change takes

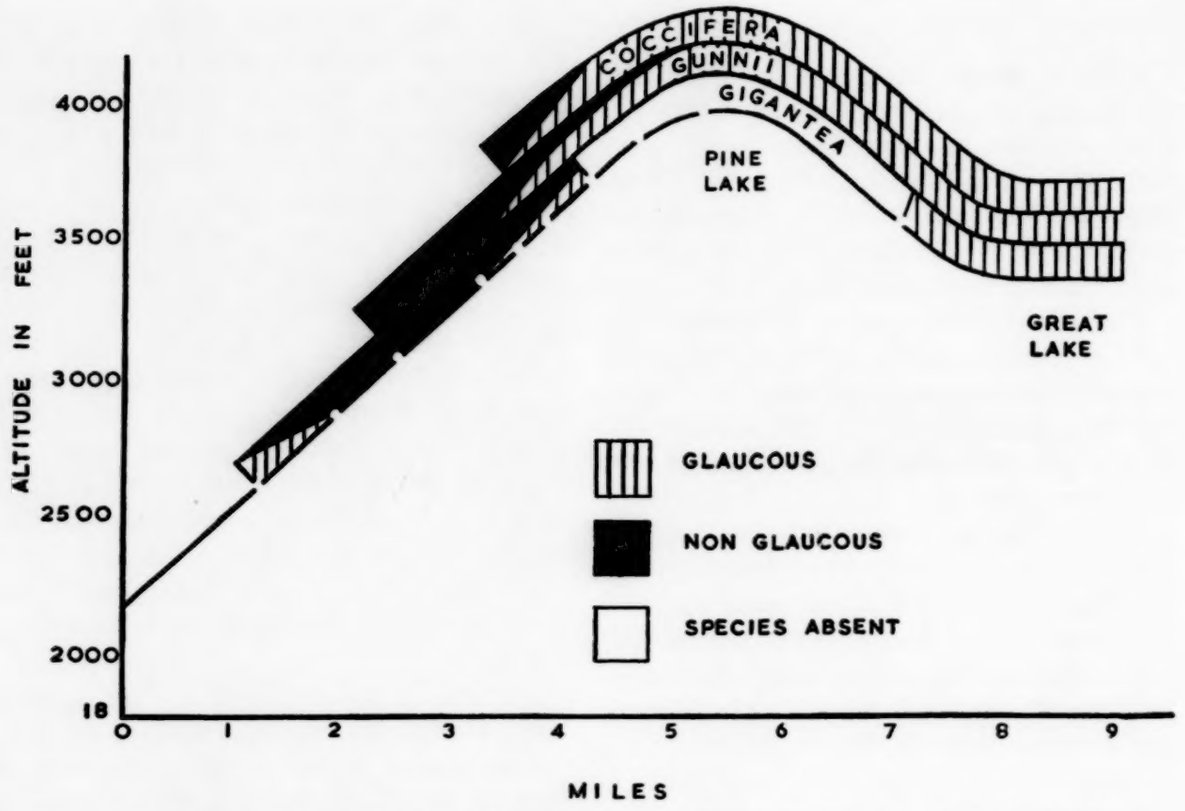

FIG. 1. Diagrammatic section from above Golden Valley to Great Lake in N. Central Tasmania to show altitudinal zonation of *Eucalyptus* species and changes in proportion of glaucous to non-glaucous saplings in each species. From about 2,800 feet to 3,500 feet the eucalypt forest is heavily penetrated by rain forest.

place, the population becoming heavily glaucous. Over a relatively narrow zone both green and glaucous trees occur in the same population. A similar clinal pattern is shown by *coccifera* on ascending Mt. Wellington (near Hobart). At 2,500 feet *coccifera* is at most subglaucous, a gradual increase in degree of glaucousness taking place over the next 1,000 feet until above 3,500 feet all trees are very glaucous. *Coccifera* probably shows such clines over the whole of its distribution area.

Gunnii shows a slightly more complex pattern. The lowest trees at 3,000 feet have green or very faintly subglaucous juvenile foliage. The adults have no glaucousness. At 3,600 feet the juvenile foliage is heavily glaucous but the adult leaves green. In the open forests round Great Lake both the juveniles and young adult type leaves are glaucous, the adult trees in spring and summer showing a beautiful mauve-grey sheen as the young leaves expand. There is, thus, a cline in glaucousness of the juvenile foliage as well as a cline in glaucousness of the young adult-type foliage. The two clines are not in step with one another.

The picture in *gigantea* is different from either of these two. *Gigantea* first appears at an altitude of just over 2,500 feet. The first populations are uniformly glaucous with the stems of saplings twenty feet high appearing as if white-washed by the heavy deposit of wax. One mile farther along the road with an increase in altitude of 100 feet red-stemmed non-glaucous saplings have reached a frequency of nearly 50 per cent. At an altitude of 2,900 feet (2 miles from the first *gigantea* populations) the frequency of white stemmed saplings has fallen to less than 1 per cent. Over the next 1,400 feet of the cline, the populations are uniformly red-stemmed but at about 3,400

feet white stemmed saplings again make their appearance. At an altitude of 3,750 feet on the north side they have reached a frequency of 60 per cent. The *gigantea* populations round Great Lake (3 miles away) are uniformly white stemmed.

A somewhat similar cline in *gigantea* exists in the forests round Tarraleah (Central Tasmania), on the road up to Cradle Mountain (N. Central) and also, though less marked, at Rose's Tier (Ben Nevis, N.E. Mountains) where no zones of pure white stemmed populations have been found.

One feature common to the two clines at Golden Valley and Tarraleah is the fact that the classification of plants is much easier at the bottom end of the cline. The segregation of white: non-white is sharp while at the top end of the cline the segregation tends to be blurred. The completely non-glaucous type has a shiny appearance as if the twigs were freshly varnished. The lowest grade of glaucous plants has a dull red appearance owing to the presence of a thin transparent layer of wax which is easily rubbed off giving a shiny varnished appearance. At the upper end of the clines there occur all grades of glaucousness from this weak grade to the full white stems.

There are also considerable differences in the degree of development of anthocyanin in the superficial tissues of the twigs at the top and bottom of the cline. Many of the glaucous trees at the lower end of the cline, have little or no anthocyanin, the stem tissues appearing light green when the glaucous wax is removed. At the upper end of the cline, the trees uniformly develop a deep anthocyanin color beneath the wax. More statistical data are needed to show whether a cline exists in anthocyanin coloration. However, the nonglaucous types are uniformly red stemmed.

Gigantea is a species widely distributed in Tasmania at altitudes of over 2,000 feet. In other areas the analysis of glaucousness is incomplete but populations, e.g., round Waratah and Guildford (N.W.) showing a local and apparently irregular variation in degree of glaucousness do occur. There are also forests showing a fairly uniform degree of glaucousness intermediate between the non-glaucous type and the full white glaucous stems so characteristic of the open forests of the Central Plateau round Great Lake. *Gunnii* also shows fairly uniform stands consisting of intermediate types on the Middlesex Plains below Cradle Mountain.

In the other species showing clinal variation, analysis is at present very incomplete but examples of clinal variation are known in all of them. *Urnigera* is a species closely related to *gunnii* and should perhaps be considered as the geographical subspecies replacing *gunnii* on the mountains of the S.W. On Mt. Wellington it shows a cline agreeing in most respects with that shown by *gunnii* above Golden Valley. At 3,400 feet, its upper limit, it is glaucous in both juvenile foliage and young adult-type leaves. At 3,000–2,700 feet the adult trees usually show no glaucousness, while the juveniles may be heavily glaucous. At 2,600 feet both adult and juvenile glaucousness are lost, the species being non-glaucous down to its lower limit of 1,800 feet.

Pauciflora is a widespread species, extending from sea-level on the East Coast to 3,400 feet round Great Lake. The pattern of glaucousness is complex but an interesting cline occurs near Lake Leake. The species first occurs about 12 miles from the E. Coast at an altitude of 1,800 feet. It comes in just before *gigantea*. At their first occurrence, both species are without stem glaucousness. But after 1 mile populations showing an intermixture of white-stemmed types occur and thereafter as the more open forests of the drier central midland savannah country are approached, the white-stemmed form replaces the red-stemmed in both species.

Salicifolia, linearis and *simmondsi* are closely related species (or subspecies), *simmondsi* replacing *salicifolia* in the

N.W., and *linearis* being almost restricted to skeletal dolerite soils below 2,000 feet in the S. and S.E. of the island. An example of a cline in *salicifolia* has already been given. The same species shows similar clines on ascending from the Central Midlands near Tunbridge to the central plateau. Clines probably occur in *simmondsi* round St. Valentine's Peak south of Burnie. In the S.E. wide-spread forests of subglaucous *linearis* and *salicifolia* occur particularly north of Buckland and along the Lake Leake Road, where both species occur in open forests.

Genetics of Glaucousness

No detailed studies of the inheritance of glaucousness in Eucalyptus have been completed. Field observations show that its inheritance is probably relatively simple (possibly a single gene difference) in some cases, e.g., the sharply discontinuous separation of glaucous : non-glaucous types in many *gigantea* and *coccifera* populations. Further the few open-pollinated progenies which have been raised in several species usually retain the glaucous grading of the mother when grown under the appropriate environmental conditions. In Hobart at sea level the maximum phenotypic expression of glaucousness in the alpine species is obtained only during the winter.

Most of these initial progenies were selected from "pure" populations and bred true. However, in *gunnii* a fully glaucous mother from Greona, Great Lake, gave a fairly sharp segregation of green and glaucous seedlings. A few seedlings were very lightly glaucous as though modifiers were segregating as well as a major gene. Glaucousness also segregates simply though multifactorially in various species crosses, e.g., *risdoni* × *salicifolia*, *subcrenulata* × *globulus*. These progeny tests will be reported in full elsewhere.

A simple inheritance of glaucousness has been reported in wheat (Watkins, 1927), *Pisum sativum* (Wellensiek, 1928), *Acacia mollissima* (Moffett, 1952) and in *Ricinus* by Peat (1928) and Harland (1947). Peat's work is of special interest in that he showed that the development of bloom depends on the presence of the dominant gene B. bb plants are green. C and D express themselves only in the presence of B and control the pattern and intensity. Bcc plants have bloom only on the stem, petioles and fruit; in BC plants the bloom extends to the under-surface of the leaf. D is apparently an intensifier. These results probably mean that the differences in pattern of glaucousness in any one species of eucalypt are also under simple genetic control. Thus the cline in *gunnii* above Golden Valley may involve a clinal change in frequency of the alleles, at, at least, two loci.

Clines and Ecological Correlations

The regularity with which these eight species of eucalypt change color is a proof that the genetic changes accompanying and causing the color changes are adaptive changes in response to selection by some ecological variable. It is true that the phenotypic variation actually observed in the field is composed of a genetic part and an environmental part. A genetically glaucous type need not always develop pronounced glaucousness; but in general it seems that the genetically most glaucous types occur in those environments which best promote the activity of the genes concerned in the synthesis of the wax. More transplant experiments are needed to prove this point but no evidence now available contradicts this conclusion.

Table 2 is an attempt to determine which ecological variable is responsible for the genetical selection which created and presumably is still maintaining the clines. Over most of the clines it is clear that there is a change in altitude which means we must consider rainfall and temperature (or frost activity) variations as possible agents in selection. The avail-

able meteorological data are both too crude and incomplete to furnish a safe guide to changes in rainfall and temperature over distances of half a mile which, as we shall see in the next section, may include a complete cline. The position is also complicated by the fact that the non-glaucous types are usually associated with the ecotone from the dense rain forest of *Nothofagus, Atherosperma,* etc., growing in regions with over 50" rainfall per annum, and the eucalypt forest in regions of lower rainfall or greater exposure. (For a detailed description of the communities see Curtis and Somerville 1949.) The development of rain forest has a great effect on the microclimates in which regeneration of eucalypts must occur. Many of the rain forest species are less frost hardy than the species growing in the much more open communities both at higher and lower elevations. In fact it is probable that the temperature fluctuations in the rain forest region are less than in the open forests. This may be particularly true with regard to the out-of-season spring frosts which are so characteristic of the Tasmanian climate except for the narrow coastal strips (Foley 1945). Above an elevation of 1,000' frosts may occur in open country in all months of the year.

In table 2 data are given for twelve clines in six different species. In all cases the change (whether increasing or decreasing) in altitude, rainfall and frost activity is indicated in going from the non-glaucous to the glaucous end of the cline. Although the data are very rough, the best correlation appears to be with frost activity, increasing frost being correlated with increased glaucousness. The table also brings out the significant association of non-glaucous types with the rain forest. The only apparent exception is *salicifolia,* which species, however, does not penetrate the rain forest zone. It is unlikely that this association is any-

TABLE 2. *Environmental correlations with clines in glaucousness in* Eucalyptus *species*

Species	Locality	Altitude	Rainfall	Frost	Rain forest	Remarks
coccifera	Mt. Wellington	→	→	→	←	
coccifera	Golden Valley to Great Lake	→	←?	→	←	Rainfall probably near maximum in clinal region
gigantea	Golden Valley to Great Lake					
	(a) lower end	←	←	→	←	Non-glaucous zone associated with maximum rain forest development
	(b) upper end	→	←?	→	←	
gigantea	Tarraleah					
	(a) lower end	←	←	→	←	Non-glaucous zone associated with maximum rain forest development
	(b) upper end	→	→?	→	←	
gigantea	Lake Leake Rd.	←	←	→	None	Little change in altitude
gunnii	Golden Valley to Great Lake	→	←?	→	←	Rainfall probably near maximum in clinal region
pauciflora	Lake Leake Rd.	←	←	→	None	Little change in altitude
salicifolia	Mathinna	→	→	→	→	Rain forest developed above salicifolia zone
salicifolia	Tunbridge-Interlaken	→	→	→	None	
urnigera	Mt. Wellington	→	→	→	←	

(1) In all cases the clinal change considered is from a non-glaucous population to a glaucous one.

(2) → means environmental factor increasing in magnitude with increasing proportion of glaucous plants in the population.

(3) ← means environmental factor decreasing in magnitude with increasing proportion of glaucous plants.

thing more than a reflection of the more equable and frost free micro-climate of the rain forest. However, it should be noted that regeneration of eucalypts in the low light intensities of the ecotone with the rain forest is dependent on some destruction of the rain forest. It may be that the non-glaucous types have some advantage under these conditions. There is no direct evidence in favor of such a supposition.

That frost is of primary importance in the survival of eucalypts in Tasmania is shown by several lines of evidence. It is clear from experiences with the planting of eucalypts in Great Britain (Martin, 1948) and in South Russia that the trees may grow for several years until an exceptionally hard winter may completely kill mature trees and plantations. Such killing frosts rarely occur in Tasmania, but there are vivid accounts (e.g., Calder, 1850 unpublished ms.) of the great frost of 1837 which killed large areas of mature eucalypt forest near Bronte (Central Plateau). The most sensitive stages in the growth of many species seem to be the juvenile stages and also the young adult type foliage. The mature foliage of such alpine species as *coccifera* is capable of being encased in ice during blizzards and then of thawing out without damage. The developing foliage in the spring is much more frost sensitive and is sometimes killed by the occurrence of a moderately severe frost after the spring growth has started. Similarly a single December frost at Rose's Tier in 1948 cut back *gigantea* seedlings and saplings particularly where the top cover had been removed by felling. Experiments have been started to determine experimentally the variation in frost resistance in the races of *urnigera, gunnii* and *gigantea*.

As regards the physiological mechanism, by which the genes controlling wax synthesis increase frost resistance, nothing is known. It is not even clear whether the development of the wax is the significant activity of these genes. Harland (1947) has, for example, demonstrated a similar cline in glaucousness in *Ricinus* in the Andes Mountains above Lima (Peru). Here he correlates the change in gene frequency with the fact that non-glaucous plants set seed throughout the year in the cloudy coastal climate, whereas the glaucous type transplanted to the coast fails to do so during the winter. However, it seems likely that the glaucous type must have some advantage at higher elevations since it completely replaces the green form about 8,000.' No differences in net reproductive rate have been observed between green and glaucous eucalypts. It is doubtful whether a direct action on the reproductive processes is responsible, either wholly or in part, for the eucalypt clines.

It is possible that the development of wax on leaves and stems may be directly responsible for increasing frost resistance. This is, perhaps, indicated by the fact that the maximum activity of the genes concerned in wax synthesis is attained only in a cold environment. Frost damage in the literature (e.g., Levitt, 1952) is often compared to dehydration injury. It may be that the glaucousness is effective in reducing water loss from the leaf at the critical growing period before the full development of the cuticle. It may also be significant that the glaucous leaves are less easily wetted by dew and rain. The solution of these problems will require further work.

Selective Forces

Haldane (1948) has given a simplified treatment of the selective forces operating within clines. He has shown that under certain conditions it is possible to determine the selective forces operating in establishing and maintaining a cline in equilibrium, either within a genetically variable species population or between two non-interbreeding species. At a habitat boundary on one side of which one type is favored, the other being favored on the other side, a cline will result by the selective differentials becoming balanced by random migration. At equi-

librium and at a sharp boundary, Haldane shows that

$$K = \frac{m^2}{2d^2} \text{ approximately,}$$

where $(1 + K)$ and $(1 - K)$ are the coefficients of selection on either side of the boundary and m = root mean square migration distance per generation and d = interquartile distance along the cline.

It is difficult to apply this formula directly to the eucalypt clines. The formula is true only for small values of K, i.e., where d is large compared with m. In *Eucalyptus* populations we have no direct measure of the migration distance but it is probably of the same order as d (see below). There is also the difficulty that the formula holds only for an ecological boundary which is sharp compared with d. Except for certain cases of edaphic control, e.g., the restriction of *linearis* to dolerite skeletal soils, the eucalypt clines are developed on a gradient of ecological factors and in many localities the steepness of this gradient will determine the steepness of the cline. However, it is, perhaps, worth comparing interquartile distances for various types of interspecific and intraspecific clines in the genus.

Before attempting this comparison, let us consider what the values of m may be. For an interspecific cline we shall be concerned only with the distance of seed dispersal per generation. For intraspecific clines as in waxy glaucousness we must also take into account the mean free path of a pollen grain. As regards seed dispersal, in all species the seeds are eventually set free by the valves of the capsule opening, the seeds being distributed by wind. The seeds are of no interest to large animals as a source of food although insects such as ants may collect them. Thus, the mean distances travelled by the seeds will depend on their weight and buoyancy, which probably vary little between the different Tasmanian species, and the height of the parental trees. It is likely that the mean migration distances will be small, perhaps about equal to the heights of the parental trees. No great differences will exist between the different species.

As regards the mean free path of the pollen grain, the distribution of pollen grains will probably be very leptokurtic owing to the variety of pollinating agents. We have no estimates of the frequency of selfing in the different species; but since most of the Tasmanian species are protandrous to the extent of several days, outcrossing is probably common. Strong flying insects such as bees and blowflies regularly visit the flowers. Large numbers of birds such as parrots and honeyeaters visit the trees in blossom and although their depredations may thin out the flowers considerably, they must act as long distance pollination. Thus, it is possible that the pollen grains may travel further than the seeds.

Let us first consider clines between two species. Some of the steepest are the aspect clines on the mudstone hills round Hobart where on the shallow soils of slopes facing north or north west, *tasmanica* or *risdoni* replace such species as *viminalis* and *obliqua* which occur on the deeper, wetter and colder soils of the Southern slopes. Direct measurement gives an interquartile distance of approximately 60 feet. Similar sharp clines occur under very different conditions on the rounded dolerite hills outcropping from the peaty buttongrass plains between Bronte and Lake St. Clair. Here the species are *pauciflora* and *gigantea*. *Pauciflora* usually forms a fringe on the lower dolerite slopes and is replaced by *gigantea* at heights of 200–300′ above the buttongrass plain. The transition is at least as sharp as in the *tasmanica* clines. The ecological control of this cline is unknown but it may be associated with frost pockets. In other cases species clines are less steep, e.g., in altitudinal zonation where interquartile distances are probably about 300–400 feet in altitude or over 1,000–2,000 feet in ground distance.

In the intraspecific clines in glaucousness the interquartile distances are also probably about 300–400 feet in altitude,

e.g., *urnigera* on Mt. Wellington, *coccifera* (Mt. Wellington and Pine Lake), *gigantea* below Pine Lake. The steepest actually measured is in *gigantea* above Golden Valley where in approximately 300′ change in altitude there is a fall in frequency of white stemmed seedlings from 100% to less than 1%.

These measurements, crude as they are, demonstrate that, although interspecific clines may show the shortest interquartile distances, the intraspecific clines do not always have the longest interquartile distances. If we take into account the fact that the relevant migration distance in an interspecific cline is simply the distance migrated by the seed, whilst in an intraspecific cline pollen migration is also operative, it seems probable that coefficients of selection of the same order are operative in building up and maintaining both intraspecific and interspecific clines in *Eucalyptus*.

Evolutionary Implications

These observations and deductions are important in several general ways. The first is the fact that an apparently "useless" characteristic of some considerable taxonomic importance has been shown to have adaptive value and to be subject to the same mechanism of evolutionary change as has been demonstrated to be operating in such diverse organisms as *Boarmia* (Ford, 1945), *Drosophila* (Dobzhansky, 1947), *Geospiza* (Lack, 1947), *Oryctolagus* (Barber, 1954), etc. In plants such changes have not usually been studied in detail, partly, one supposes, because the mutational origin of species by polyploidy tends to obscure the issues of continuous selective change and partly because the estimation of variability is so much more difficult in plants than in animals. It is all too easy in a plant population to put down the variations one sees to the result of variations of environment, not of genotype. Another reason is, perhaps, the preoccupation of botanists with various sorts of hybrid analysis usually based solely on the *phenotypes* of wild populations. For example, Stebbins (1950, pp. 61, 255), in his discussion of conditions in *Quercus* where, as in *Eucalyptus,* the complication of polyploidy is absent, starts by saying that many species are polytypic and that hybrid swarms are common between related species. Most of the analysis is devoted to hybrid swarms and "introgression," the polytypic variation being dismissed as due to Sewall Wright's random gene fixation in small partially isolated populations. Both types of variation are presumably useless to the species at the present day except in that they may preserve evolutionary plasticity for the future. In this type of analysis, the *origin* of genetic variation by mutation, migration or chance is stressed rather than its utilization in some selective adaptive change and little consideration is given to mechanisms, such as heterosis, ecotypic diversification etc., which may conserve genetic variability at a high level for an indefinite period.

As regards the origin of the genetic variability used by these eight species of eucalypt in their parallel adaptive changes, it is tempting to suppose it was derived from some sort of introgression process, the relevant genotype having been selected out of the segregating population resulting from interspecific hybridization. Such processes undoubtedly occur in *Eucalyptus* (Brett, 1937; Pryor, 1950). However, it is unlikely, for several reasons, that introgression can have supplied the necessary variability except, perhaps, in isolated cases. In the first place, Anderson (1949) has shown that introgression usually leads to several characteristics showing correlated variation. In the eucalypts, there is little evidence of such correlated variation. Further, it now seems clear that at least one major genetic sterility barrier exists within the genus. In Tasmania no instance of hybridization between the two subgenera Renantherae and Macrantherae has been observed. If such hybridization

did occur, it would presumably show itself in intermediate types of anther (cf. Pryor, 1953) and in mixed oil types. In Tasmania both characteristics seem absolute with no intermediates. If this barrier to crossing does exist, it means that the variation pattern in glaucousness has been independently developed at least twice, once in the Macrantherae and once in the Renantherae (see table 1). The fact that the chemical characteristics of the wax vary in the different groups of the Renantherae may indicate at least a double origin within this group. These are minimum estimates since the significance of rare hybridization within both the Macrantherae and Renantherae is still problematical. It is worth noting in this connection that interspecific hybridization has been proved to be possible between non-glaucous species, e.g., *subcrenulata,* and glacous, e.g., *globulus,* both in nature (Brett, 1937; Barber and Jackson, unpubl.) and artificially (Martin, unpubl.). Neither species has been observed to use this "introgressive" variability in the development of adaptive selection clines.

There is, indeed, some slight evidence that, within the one species, e.g., *gigantea* or *gunnii,* two genetic mechanisms may exist controlling degree of glaucousness. Although accurate estimates are difficult and depend on growing progenies under uniform conditions, in some populations, as we have seen, scoring glaucous : non-glaucous plants is easy; in others it is difficult owing to the degree of glaucousness varying continuously. In the first case, it is as if a single major gene were segregating; in the others as through several polygenes with approximately equal and additive effects were segregating.

Thus we must conclude that, in general, the genetic variability used in these adaptive processes has arisen independently within each of the species populations. Its origin is presumably to be sought in the slow but continuous rate of adaptively random gene mutation in these large populations. However, as Darwin showed in 1859, the adaptive utilization of genetic variability is the all important problem from the point of view of evolutionary mechanisms, not the origin of that variation.

There is a further important point. The development of glaucousness is, of course, not the only method of increasing frost resistance open to a eucalypt species. This is shown by the lack of correlation of frost hardiness and glaucousness between different species. It is rather as if glaucousness is developed to extract the last potentialities of the species genotype as regards frost resistance. The differences in frost resistance between say *globulus* and *vernicosa* must depend on something other than glaucousness. These differences may be less subject to genetic variability than is glaucousness. They may, perhaps, be equated to the "protoplasmic factors" in frost resistance (Scarth 1944) such as reduced structural viscosity, increased formation of soluble proteins, etc., in response to colder conditions. Such other mechanisms for increasing cold resistance are undoubtedly under genic control, but their investigation in *Eucalyptus* has not so far been attempted.

Summary

1. The appearance of glaucousness on stems and leaves in *Eucalyptus* is shown to result from either the deposition of wax on the epidermis or from structural features of the superficial tissues.

2. The melting point of the wax is apparently correlated with other classical taxonomic characteristics.

3. Variation in glaucousness within a species is either sporadic and the result of mutation and occasional hybridization, or it is clinal.

4. The clines in glaucousness are correlated with changes in frost activity, the more glaucous populations occurring in the more frosty localities. Parallel clinal variation has been observed in eight species.

5. Whilst the detailed inheritance of glaucousness has not been worked out, it is clear from transplant experiments and other evidence that the clines in glaucousness represent changes in allelic frequencies at one or more loci controlling the development of wax.

6. The clines are the result of natural selection favoring the survival and reproduction of genotypes capable of developing waxy glaucousness in the more frosty regions of the species range.

7. A comparison is made of the steepness of the clines between genetically isolated species and these intra-specific clines in glaucousness. It appears probable from such comparisons that the forces of selection which create and maintain the clines are of the same order in the two cases.

8. From a consideration of sterility barriers within the genus and other evidence, it appears unlikely that the parallel variation in glaucousness has arisen by any process of introgression. Similar environmental stresses have evoked similar adaptations in a number of related but reproductively isolated species populations.

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EVOLUTION OF CLIMATIC ADAPTATION IN HOMEOTHERMS[1]

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Climatic adaptation in warm-blooded animals has been a subject of much concern to ecologists and evolutionists. With the formulation of the climatic rules of Bergmann and Allen it has become almost dogma that a reduction in the surface area relative to weight is a morphogenic factor of prime importance in the evolution of cold-hardy species or races. This idea is based on the simple reasoning that, other factors being equal, the less surface area an animal has the less heat it would lose. Natural selection would therefore favor an arctic fauna tending towards large globular woolly balls with the least possible ears, tail, snout and legs. Tropical animals would tend in the opposite direction, towards smaller skinny forms, with long legs, snout, ears and tail. Clines of this sort have been looked for and have been found in many mammals and birds, and are given in textbooks on evolution as classical examples of the workings of adaptation by selection. Lately anthropologists have seen in the climatic rules a powerful tool by which to explain many racial features in man.

Adaptation, in the sense of "rendered fit for," implies an understanding of how and why the observed trend or response is useful, and is hence linked up with physiology. Sufficient information on the physiological adjustments of arctic and tropical animals is now available so that we may attempt an analysis of what phylogenetic pathways evolution has actually followed in the engineering of climatic adaptation of warm-blooded animals.

[1] Contribution No. 755 from the Woods Hole Oceanographic Institution.

CLIMATIC ADAPTATIONS FOUND IN ARCTIC AND TROPICAL MAMMALS AND BIRDS

Most homeothermic animals require maintenance of a constant internal body temperature. This is generally higher than the environmental temperature. In arctic latitudes the temperature gradient to the outside is so great that the main problem becomes one of keeping warm. Thermally speaking there are three avenues open for adaptation to the arctic environment: (1) by lowering the gradient, (2) by increasing the heat production, and (3) by decreasing the heat dissipation. In a tropical environment overheating would be checked by changes in the opposite direction.

It is known that the body temperature is the same in species from all climates. (Compare Morrison and Ryser, 1952, and Irving and Krog, 1954.) Also the basal heat production has been found to be essentially the same in all climates, inasmuch as most arctic, temperate and tropical mammals fit the mouse-to-elephant curve of Benedict (1938). Birds show this regularity too. This leaves the heat dissipation as the only major avenue for phylogenetic adaptation to climate. (Compare the three papers by Scholander, Hock, Walters, Johnson and Irving, 1950.)

Major adaptations are traceable not only in the overall heat dissipation but also in the heat dissipation of localized peripheral structures. We shall consider the overall heat dissipation first.

ADAPTATION OF THE OVERALL HEAT DISSIPATION

At thermal equilibrium the heat dissipation balances the heat production.

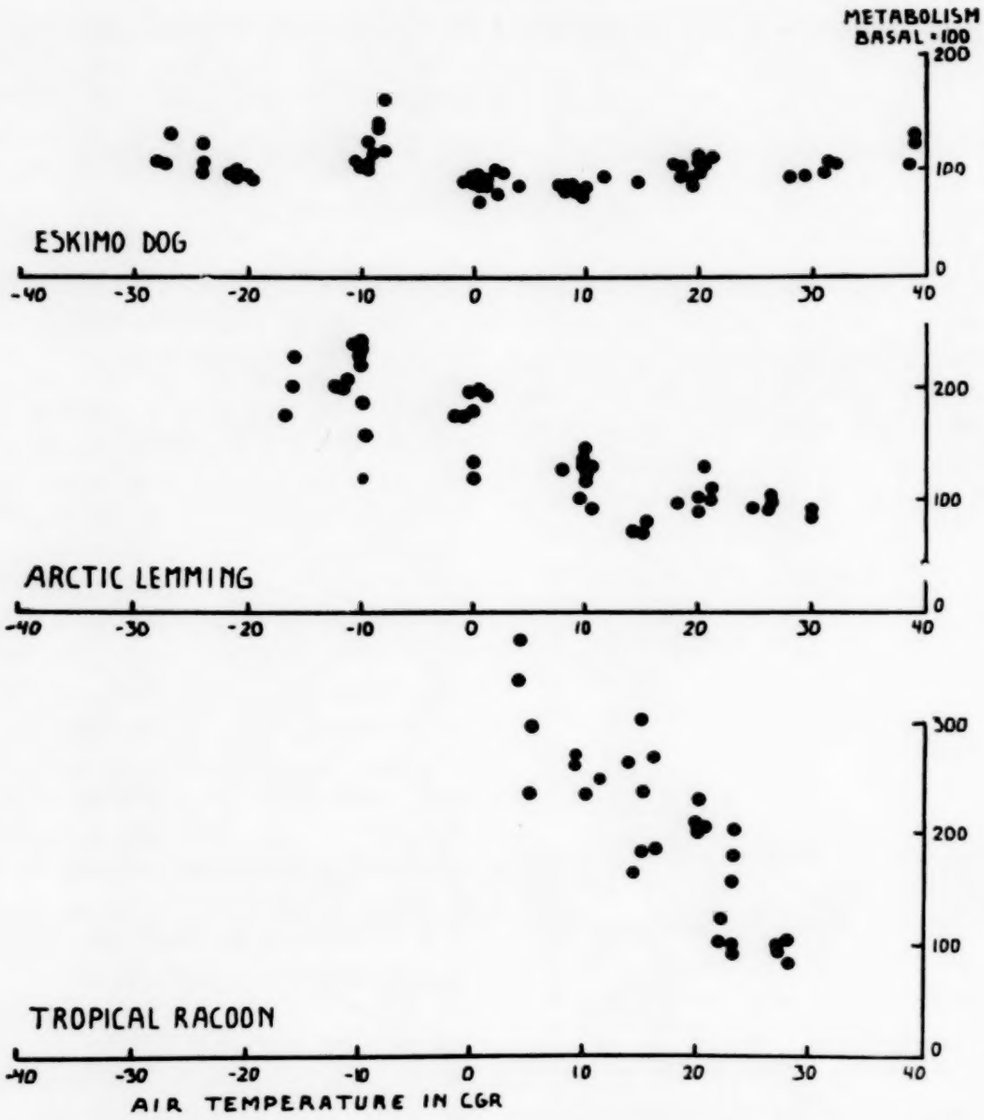


FIG. 1. Heat production versus environmental temperature in the husky, the lemming and the tropical racoon. Resting or basal rate is set at 100. Critical temperature is below −30° in the husky, 10–15° in the lemming and 25–27° in the tropical racoon. (From Scholander, Hock, Walters, Johnson and Irving 1950.)

The latter is usually determined indirectly from the oxygen consumption or the carbon dioxide output. It is reasonable to assume that a mammal or a bird when fully adapted to its normal environment can rest and sleep in it at essentially basal heat production. A fundamental measure of the overall adaptation to cold is therefore to determine the lowest air temperature at which the animal can maintain a resting or basal metabolic rate, without losing body temperature. This is its *critical temperature*.

If the temperature of the environment drops, our resting mammal or bird will compensate for it by decreasing the heat loss. This is done by raising hairs or feathers, decreasing peripheral circulation and by balling up. At the critical temperature the overall insulation has reached its maximal value. If the environmental temperature is lowered still further, shivering sets in as a gross sign of incipient metabolic heat regulation. From this point on there is an increase in the heat production which is approximately proportional to the difference between the body and air temperature, such as would be expected from Newton's law of cooling (cp. fig. 1).

In tropical mammals the critical temperature was found to be 25–27° C., the same as in naked man. In the arctic fox and husky the critical temperature was not yet reached at − 30° in laboratory experiments. In these and larger arctic mammals it is probably − 40° or lower since they can sleep unprotected on the snow at these temperatures. When curled up on the snow they may be likened to a man resting comfortably in an arctic sleeping bag at −40°.

Mammals and birds smaller than a rabbit have critical temperatures higher than the larger animals. Lemmings had a critical temperature of around +10° and a little shrew with much less body insulation must have one still higher. These and many other small mammals live in the cold northern forests or on the tundra through the winter, but they all seek shelter, often under the snow, where microclimates may be found which are only a few degrees below freezing (Johnson, 1951). Many of them build warm nests. If shelter is not available such small animals may have to pull through cold spells by sustained high metabolic rate. Snow buntings were kept outside in an open wire cage at Point Barrow, Alaska, during the whole winter. These birds had a critical temperature of 0° and nevertheless spent several months at − 20° or lower. They normally migrate south in the winter.

In humans the critical temperature is only known for the white man and is about 27°. In spite of much recent work on the Eskimo this, his most fundamental index of overall temperature adaptation, has not been determined. Neither has the microclimate inside his clothing or sleep-

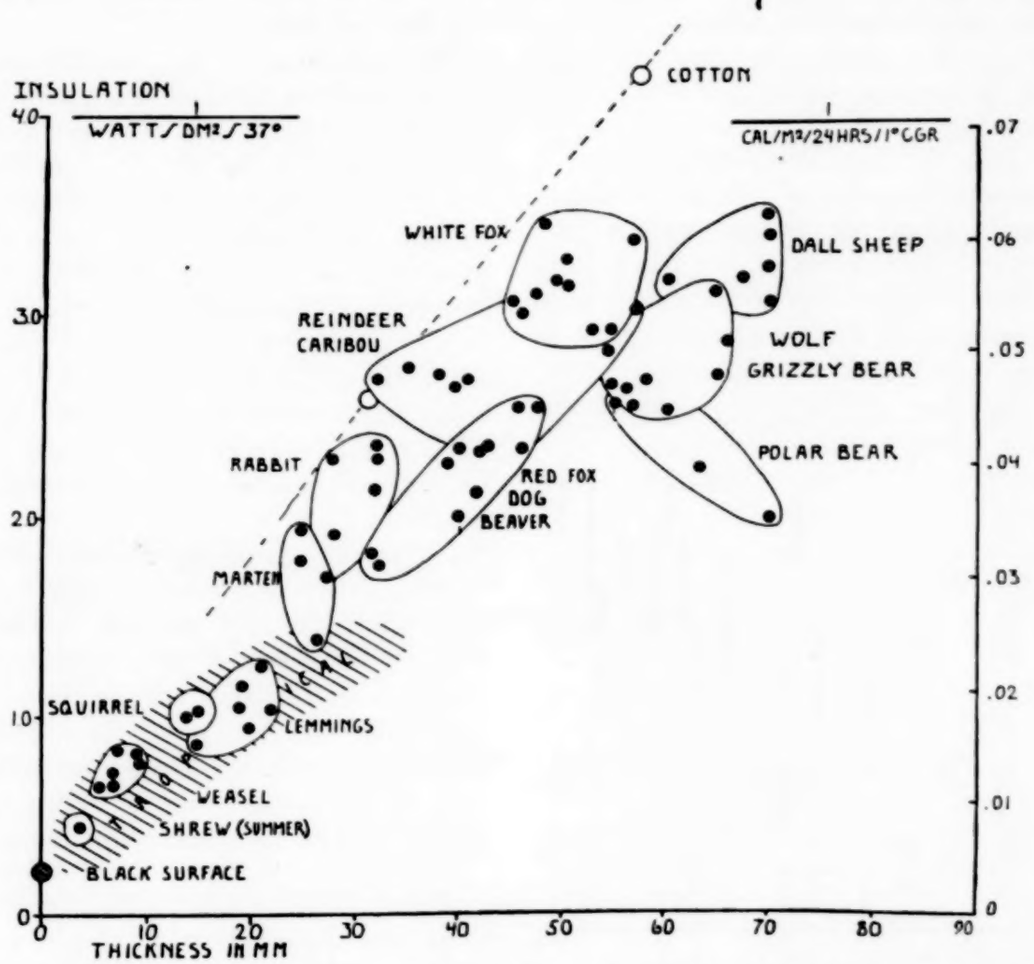


FIG. 2. Insulation of winter fur from arctic and tropical mammals. (Modified from Scholander, Walters, Hock, and Irving, 1950.)

ing bags been defined, but it is most likely as warm as ours. At least, his mittens, footwear and other clothing are excellent and sufficient to keep us warm. The really cold people, such as the Tierra del Fuegians of former days, or the Australian aborigines, have not been tested conclusively. Hicks, Moore, and Eldridge (1934) found that the Australians were able to rest at a basal heat production naked at 0° air temperature, but as they were surrounded by little fires their environmental temperature is unknown (Goldby, Hicks, O'Conno. and Sinclair, 1938).

How have the observed great differences in the critical temperature come about? There are two major avenues available. One is the increase in body insulation as we go towards colder climates; another is an adaptation of extremities and other peripheral parts to tolerate, and remain functional at, low tissue temperatures, sometimes even approaching zero degrees.

Body Insulation

Measurement of the body insulation of mammals from the tropics to the arctic, on detached pieces of fur taken from the trunk, shows that it increases from warmer to colder climates (fig. 2). In arctic mammals the trunk insulation increases from the shrew to the rabbit, but from then on as the animals get bigger the insulation remains approximately constant (fig. 3). In the same environment a 5 kg hare or fox has about the same insulation as a 500 kg moose. For these animals the body-to-air gradient is the same, and hence the heat transfer per surface area should be about the same. This may be derived independently from the fact that the resting metabolic rate of a mammal is in general roughly proportional to the $\frac{3}{4}$ power of the weight (Brody and Procter, 1932; Brody, 1945; Kleiber, 1932, 1947). This makes it close enough to be proportional also to the $\frac{2}{3}$ power of the weight, which is the relationship the surface area bears to weight. We should therefore not be surprised to find about the same insulation in all of the larger arctic species, including fur-clad man.

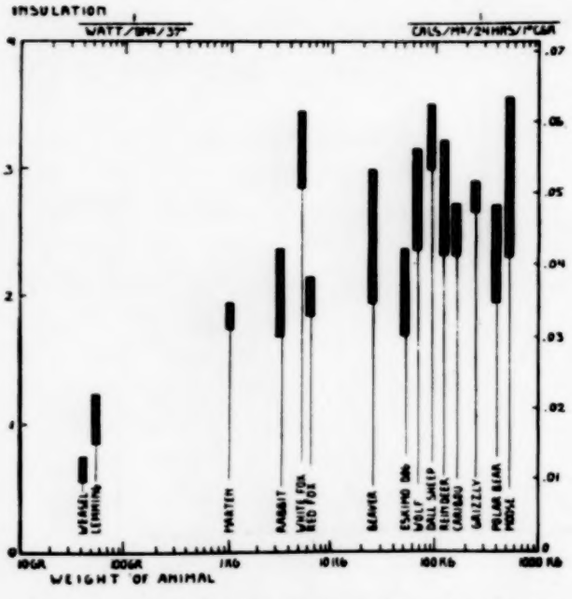


Fig. 3. Insulation of the winter fur versus size of arctic mammals. (From Scholander, Walters, Hock, and Irving, 1950.)

The non-adaptability of the resting rate shows that the heat production is not determined by the heat loss, as one might infer from the surface law of Rubner (1883), but vice versa. Whatever the surface area happens to be, the heat loss from it must be so regulated by various means that it balances the heat production. In a homeotherm one might say that body temperature plays the first violin, metabolic rate the second, and heat loss the third. The surface area is but one of the several factors which determine the heat loss.

In tropical animals the body insulation varies from almost complete nakedness to a sizeable amount of fur. A tropical sloth has a fur on its trunk as warm as that of an arctic lemming. This somewhat astounding fact is undoubtedly linked up with the very low metabolic rate of the sloth, which is no more than half of that of an ordinary mammal.

Adaptation in Peripheral Parts

It was shown that an arctic mammal like the husky or fox may sleep on the snow at $-40°$ at a resting metabolic rate (fig. 1). This is possible because of the

very high overall body insulation. If this animal were to get up and run, let us say on a warm sunny winter day, it would have to increase suddenly its heat dissipation by some 10 to 20 times, in order not to heat up. Such a latitude in heat dissipation cannot be accomplished through the dense, thick body fur, but is achieved by other means. All arctic mammals and birds present a conspicuously uneven insulation. The extremities and face are generally very poorly insulated; in most mammals this is also true for the belly. A caribou, reindeer, or mountain sheep has three to five times less insulation on the legs than on the trunk (Scholander, Walters, Hock, and Irving, 1950).

It is a reasonable assumption that these poorly insulated parts, when warmed by increased circulation, would serve as essential avenues for an increased heat loss. Penguins and seals when out of water may keep their feet and flippers very hot, and seals are known to have an extremely efficient vasomotor control in the flippers (Scholander, 1940; Irving, Scholander, and Grinnell, 1942). Arctic sea gulls (*Larus glaucus*) avoid freezing their legs in subzero weather by increased circulation (Scholander, Walters, Hock, and Irving, 1950). Panting and exposure of the tongue are other well known avenues for increased heat dissipation.

When heat must be conserved the bare areas or parts may cool very considerably. This has been shown by measuring the leg temperature in many arctic mammals and birds (Irving, 1951). In cold weather reindeer and huskies and other arctic mammals and birds maintained their legs at 10° C. or even lower for prolonged periods. When resting, the animals usually coil up, shielding the bare parts from the cold.

Many species of more or less aquatic mammals and birds keep their naked feet, and sometimes the tail, in ice water for a long time. We may mention ducks, sea gulls, penguins, wading birds, whales, seals, beavers, muskrats, otters, moose and others. Some of these have greatly expanded flukes, fins, flippers or webbed feet. Temperature records from these structures are few. Irving found, however, that the feet of sea gulls (*Larus argentatus* and *L. glaucescens*) may be kept near zero degrees (Chatfield, Lyman, and Irving, 1953). When the feet of an arctic gull (*L. glaucus*) were kept in a thermous bottle of ice water their caloric output over two hours was only 1.5% of the basal rate of the bird. (Scholander, Walters, Hock, and Irving, 1950). From the handling of subarctic porpoises (*Phocaena*) in cold water and young arctic seals (*Cystophora*) in ice water it is known that their flukes or flippers may keep close to the water temperature (personal observations). It would be difficult to conceive how much animals could remain warm if they had to keep these expanded and thin organs at body temperature in the ice water.

As a corollary to the conspicuously low temperature which we may find in peripheral parts the nerves in the cold tolerant legs of a herring gull were found to conduct impulses at temperatures so low as to render the nerves of a hen's leg useless (Chatfield, Lyman, and Irving, 1953).

Vascular Heat Exchangers

Many mammals and birds show a vascular pattern in the extremities or other peripheral parts which may be interpreted as an adaptation to heat conservation. Claude Bernard (1876) considered that some of the heat from the arteries would be transmitted over to the cooler blood returning through the neighbor-

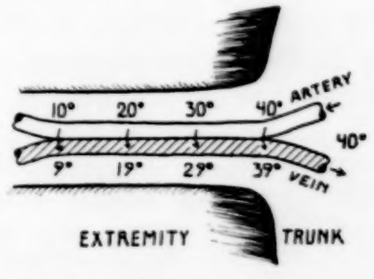
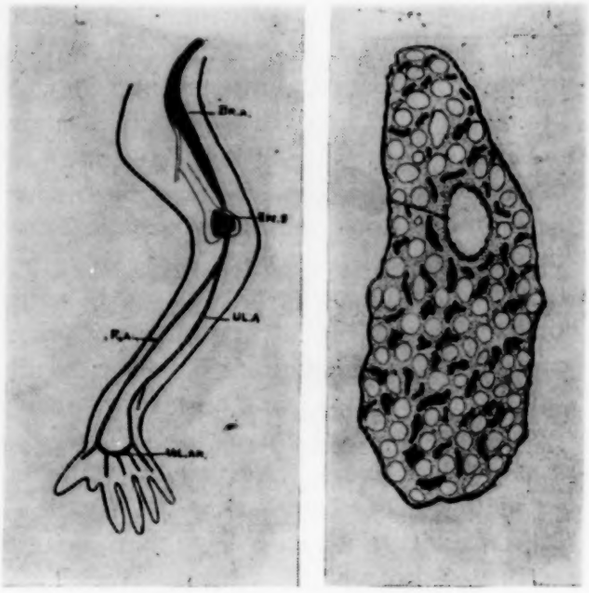


Fig. 4. Schematic presentation of arteriovenous counter current heat exchange in an extremity, resulting in a steep linear temperature gradient and consequent reduced peripheral heat loss.

ing veins. Bazett and his coworkers (1948) through numerous measurements in man showed that temperature gradients of as much as 3 degrees per decimeter could develop along a brachial or radial artery, mainly because of heat transfer from the artery across to the *venae commitantes.* The principle of operation of such a counter current exchange system will be seen from the diagram in figure 4.[2] The heat exchange system as we find it in man is a mere rudiment compared to those we find in many mammals and birds. The multichannel arteriovenous *rete* systems to be described below are by physical necessity heat exchangers and economizers of the body heat. Whether or not this is their primary or sole function is another matter.

In the manatee the flippers and tail are supplied with blood through a bundle of hundreds of arteries and veins intermingled in a *rete* (Murie, 1872; Fawcett, 1942). Fan-shaped arteriovenous bundles are prevalent in the peripheral structures of seals (Zuckerkandl, 1894; Müller, 1904; and personal observations). The tail and flippers of whales are supplied through arterio-venous *retes* (Stannius, 1841; Wilson, 1879; Braun, 1905; Slijper, 1936; Fawcett, 1942). The arteries in the tail fluke are surrounded by venous channels (personal observations). The capybara and to less extent the nutria, amphibious rodents of South America, have arteriovenous *retes* in the legs (Müller, 1904).

Penguins have an arterial *rete* in the axilla suggestive of heat exchange with the veins, which are fewer in number (Watson, 1883; Müller, 1908). Tall wading birds like cranes, herons, flamingos have tarsial arterio-venous *retes,* as



A B

FIG. 5. A. Arm of loris (*Loris lyddekerianus*) with brachial vascular bundle. B. Section of the hind leg bundle; arteries white, veins black. (From Rau and Rao, 1930.)

have also several long-legged land birds (Hyrtl, 1863). Sea or lake waters are cooling even in the tropics, considering that the cooling power of water is some 20 to 50 times that of air of the same temperature.

Many terrestrial tropical mammals have arterio-venous bundles running out into the extremities and tail instead of, or in addition to, the conventional single arteries with their *venae* commitantes (fig. 5). The most striking development of such bundles or *retes* is found in sloths, anteaters, armadillos, pangolins, loris, tarsiers, and monotremes (Hyrtl, 1853, 1854; Zuckerkandl, 1894, 1895, 1907; Leche and Göppert, 1902–1906; Müller, 1904; Wislocki, 1928; Rau and Rao, 1930; Wislocki and Straus, 1932; Davies, 1947). Of these animals the sloth is known to be extremely temperature sensitive, and at times it may well need to keep its long arms and legs at a low reptilian temperature to be able to keep the trunk warm. Its resting metabolic rate is only half that of an ordinary mammal (Scholander, Hock, Walters, and Irving, 1950).

[2] The theory for a multi-channel counter current exchange system of this sort has been elaborated for the *rete mirabile* of the swimbladder of deep sea fishes. Here an oxygen gradient of some 100–200 atmospheres is maintained across the swimbladder wall, and the *rete* can be calculated to cut down the oxygen tension of the leaving blood to only a few millimeters of mercury (Scholander, 1954).

Monotremes are normally very temperature sensitive in their metabolic response to cold and have a low metabolic rate (Martin, 1902). The loris are very sluggish animals.

Other animals, such as ducks, geese, swans, sea gulls, have not been found to have macroscopic heat exchangers in their legs (Hyrtl, 1863), although one might well at first thought expect that they would need them. Irving found a steep temperature gradient below the feathered part of the leg in a sea gull (*L. glaucescens*) suggestive of a vascular heat exchange mechanism (Chatfield, Lyman, and Irving, 1953).

In any attempt to evaluate the thermal significance of the *retes,* one must remember that in well insulated animals, like the fox, which is capable of sleeping on the snow at $-40°$, there may arise a serious problem of heat dissipation, when the weather turns warm, or when the animal is running. Where heat conservation is the main problem one might find vascular heat exchangers; where heat dissipation is the more important point one might not find them. Final evaluation of the thermal significance of these striking structures must of course await experimental measurements. At all events the extremities and sometimes the tail and other bare parts of the body are essential for the heat regulation in northern species and show very significant adaptations to climate.

Bergmann's and Allen's Rules

In the above brief outline of known physiological pathways in the phylogenetic adaptation to hot and cold climates no mention is made of the possible importance of the overall size of the animal. Neither is there any reference to the absolute or relative size of the protruding parts such as legs, tail, and ears. Behind both Bergmann's and Allen's rules lies the idea that as we go to colder environments the surface of animals relative to weight should become reduced, bringing about a decrease in heat loss. These rules are conceived as applicable primarily on a sub-species level. (Compare Goldschmidt, 1940; Huxley, 1943.) There are two aspects here which are of interest to us: To what extent are clines of this sort of general occurrence, and what evidence is there that they are caused by a physiological response to cold?

To the first question one may point out that there is disagreement as to whether these clines constitute clear trends. Rensch (1936) is the chief proponent of the validity of the rules, whereas Reinig (1939) denies them, finding size clines radiating more or less in any direction from a common distribution center. Well-known cases where size increases southwards are among many others, the puma, the racoon and the otter (Allen, 1906). The rules evidently are not entirely above debate. For the physiological interpretation of established cases this does not matter a great deal, inasmuch as the basic measurements are often thermally irrelevant or reveal differences so small that they cannot be appraised.

The Biometrical Data. In the arguments for the validity of Bergmann's and Allen's rules Rensch has, for example, made use of data from Ridgeway's "The Birds of North and Middle America" (1904–1914). The measurements are based on dried museum skins. The size is taken as the wing length, which is the length from the wrist bend to the tip of the longest primary. There are a few short finger bones in this measurement, the rest is just wing feathers. These measurements may correlate with flight but bear no useful thermal significance. If we consider a five millimeter's difference in length of these feathers as thermally uninterpretable we find that 16 subspecies pairs out of a total of 43 have slightly longer feathers going north. If we consider it uninterpretable whether the tarsus is 30% or 32% of the length of the wing feathers then also Allen's rule disappears from physiology.

Rensch also compared subspecies pairs of southern and northern mammals based on skin measurements given in Anthony's "Field Book of North American Mammals" (1928). In a series of 30 pairs 80% of the subspecies were longer in the north; in a similar series of European forms 60% were longer in the north. The length difference was mostly less than 10%. The relative length of feet and tail versus body length was often a trifle smaller in the northern form of a pair. The correlation was considered positive at a difference of only 0.2% (i.e., 20.0% instead of 20.2%).

Physiological Significance. If, contrary to the view of Reinig, the slight biometrical trends found by Rensch are taken to reflect a general tendency, what is the evidence that they represent a physiological adaptation to temperature?

Exposure and resulting adaptation to cold do, of course, affect the whole population of northern mammals and birds. From a purely physiological standpoint, if relative surface reduction were a point of general adaptive importance, we should expect this to modify the animals not only on a subspecific level, but the whole northern warm-blooded fauna should by convergence tend towards large globular species. This quite obviously is not so. In some of the coldest areas on earth, the great northern Canadian and Siberian forests, there is a wide variety of sizes and shapes in both birds and mammals. There are little birds with naked legs thinner than match sticks, such as redpolls and chickadees, there are tiny shrews and mice, there are long-tailed foxes, long-legged, long-eared mammals, like the moose and deer. Some of the mammals of the cold forests or tundra have a considerable expanse of horns.

In the icy polar lakes and seas swim mammals and birds, such as whales, seals, and penguins, not with surface-saving, reduced extremities but with legs or tail naked and expanded into swimming surfaces. We also find numerous wading birds walking about with their tall, thin legs in ice water. Nowhere are extremities so regularly exposed to more severe chilling. Yet here we find no tangible evidence that the size of the surface area, absolute or relative, is in any way a critical factor in arctic or northern phylogenetic adaptation.[3] The prime point is *conservation of heat,* true enough, but in this the size of the surface area of the animal is of minor importance, at best. The factors that count are the *thermal properties of the surface*—its insulation, its exposure, its vascularization, and its ability to tolerate a cold tissue temperature. Poorly insulated and expanded areas do not disappear but are essential adjuncts in heavily insulated animals which ensure sufficient latitude in the heat regulation.

In the tropics the assortment of mammals and birds is similar to that in the arctic, but less well insulated. There are tiny birds and large ones, tiny mammals and large ones, some chubby and stocky like the rhinoceros, others long and lanky like the giraffe.

We are unable to see any evidence that the surface area as such has played a detectable role in the phylogenetic engineering of warm-blooded animals for hot and cold climates. The heat loss from the available surfaces, as a function of their insulation, their exposure and their surface temperature, drowns out in importance the numerical value of the areas.[4]

We may conclude that there is no physiological evidence to indicate that those cases of subspecific clines which accord with Bergmann's and Allen's rules

[3] The hopeless inadequacy of cold adaptation via Bergmann's rule may be seen by the following consideration. Take a body-to-air gradient in the tropics of 7° and in the arctic of 70°, i.e., a tenfold increase. A tenfold greater cooling in the arctic animal is prevented by covering the surface with fur a few centimeters thick. A relative surface reduction of ten times would require a weight increase of the animal of one thousand times.

[4] For these same reasons it is conceptually an unfortunate custom to express basal or resting metabolic rate as per surface area.

are the result of a heat-conserving adaptation. One must be open for other interpretations. Cold climates do not produce a fauna tending towards large-sized globular forms with small protruding parts. The phylogenetic adaptation to heat conservation in the arctic took place through other means, which have been measured, which are understood, and which apply to every individual of every species.

Bergmann's and Allen's Rules Applied to Man

Hardly anywhere have these "rules" been taken more seriously than in modern anthropology. Coon, Garn and Birdsell (1950) in their stimulating book "Races. A Study of the Problems of Race Formation in Man" take the racial features of many people to be the result of an interaction between the climate and the surface area of man.

The stockiness and relatively short extremities found in many Eskimos are interpreted as the result of cold, working through generations on the hands and feet of these people, giving short-limbedness a selective advantage. Similarly the Mongolian face has been engineered by the cold wind and weather. This is evidently based on the concept that the Eskimo is a people perpetually shivering from cold. As already mentioned, there are no measurements to substantiate such an idea. They are clever in clothing. You are warm when you stay with them and when you use their mittens and leg wear. Furthermore, it would seem that tall Eskimos could easily cheat evolution out of shortening arms and legs simply by getting long enough sleeves on their parkas and long enough legs on their pants. Extra mittens and socks could also be had if needed. Where then would be the stimulus to drive the selection?

If subjected to a suitable cold stress, circulation will improve in our hands and feet so that they may remain warm and functional at an exposure which would render unadapted digits numb and useless (Balke, Cremer, Kramer, and Reichel, 1944; Carlson, Burns, Holmes, and Webb, 1953). In Eskimos adapted hands remain conspicuously well circulated and warm on cold exposure (Brown and Page, 1952, and personal observations in the field). This is a heat-wasting tropical type of emergency reaction. In sharp contrast to this we have the heat-preserving, cold, but functional extremities of arctic mammals and birds. This ultimate adaptation evolved in animals compelled to submit to the environment. In the Eskimo the main adaptation lies not in physiology, but in an age-long experience and technical skill in ducking the cold. They conquered the arctic not by submitting to it but by surrounding themselves successfully with a little piece of the same tropical microclimate upon which we also depend.

As the opposite of the allegedly cold-engineered Eskimos the tall Tuaregs of the hot and dry Sahara have been cited, and with them the Australian aborigines. Several tribes of the latter were studied by Hicks, Moore, and Eldridge (1934), who observed that these *naked* people expose themselves seasonally to very low, even freezing, temperatures, something neither we nor an Eskimo would ever venture to do naked. This certainly confuses the idea that the Eskimo features are a result of cold exposure and the Australian features a result of heat exposure. There is hardly any valid evidence from physiology that the surface area as such, in man or beast, is a factor of general morphogenic importance in the evolution of races inhabiting hot or cold climates.

Summary

Mammals and birds have the same body temperature in hot and cold climates, and within the same weight range they have roughly the same basal heat production per unit weight. This leaves them with *heat dissipation* as the only

main avenue for climatic thermal adaptation. The lowest air temperature at which a mammal or bird can rest at a basal heat production, maintaining its body temperature, is the critical temperature. This is 25–27° in naked man and in many tropical species, and −40° in the larger arctic species, and is a fundamental measure of the overall climatic thermal adaptation. The major reason for the low critical temperature in the arctic species is the heavy body insulation provided by fur or feather coats, combined with an outstanding tolerance of low tissue temperature (often near 0°) in poorly insulated peripheral parts such as legs, tail and face. There are good indications that arctic species depend upon vascular control of these poorly insulated parts for heat dissipation. Without them they would over-heat during exercise when the heat output may be increased 10–20 times over the resting rate. Aquatic species, especially, expose their naked feet, fins or tail to the most severe chilling in ice water. Yet these organs are usually thin and greatly expanded for swimming. In many arctic and tropical species cold extremities, and consequently low heat loss, are assured by arterio-venous counter current heat exchangers at the base of the limbs or tail. In spite of the low temperature which may prevail in the extremities when the animal needs heat conservation, these organs are fully functional.

There is no physiological evidence, in beast or man, that the minor and erratic subspecific trends expressed in Bergmann's and Allen's rules reflect phylogenetic pathways of heat-conserving adaptation. Arctic species do not tend towards large spheres with reduced extremities and tail. The phylogenetic adaptations which have taken place are fairly well known in their main physiological aspects, as outlined above. They are major and general, as is the stimulus of the climate, and they know no taxonomic barriers.

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THE EFFECTS OF POPULATION DENSITY AND COMPOSITION ON VIABILITY IN *DROSOPHILA MELANOGASTER*

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INTRODUCTION

The ability of organisms of a given genotype, relative to that of other genotypes, to transmit their genes to future generations has been shown repeatedly to be a function of the environment in which these organisms develop and reproduce. This ability, the adaptive value of the genotype, may vary markedly from one environment to another or may be quite uniform under a wide variety of environmental circumstances. A striking illustration of this can be found in the work of Dobzhansky and Spassky (1944). These authors investigated the viability, from egg to adult, of a number of genotypes isolated from natural populations of *Drosophila pseudoobscura,* when the larvae were raised at three different temperatures. While some genotypes showed no difference in larval survival from one temperature to another, others showed distinct differences. Thus, one genotype, although lethal at 25.5°C., showed a nearly normal larval survival at 16.5° C.

The dependence of the adaptive value of a genotype on the environment should extend to biotic as well as physical factors of the ecology. Indeed, a large portion of ecological research has been devoted to studies on the interrelation of species as well as on the effect of varying population densities within a species. The relative abundance of a species is dependent upon the kind and abundance of other species around it. Moreover, the abundance of a given species at one stage of its life cycle is a function, and often not a simple function, of its abundance at a previous stage. It would be strange if what applied to different species did not apply to some extent to different genotypes within the same species.

Although it would seem probable that the adaptive value of a genotype is a function of the presence and relative frequencies of other genotypes coexisting with it, the study of this dependence has been neglected. Some information does exist on the role played by population density in determining the relative values of genotypes. Thus Timofeef-Ressovsky (1934) and Dobzhansky and Spassky (1944) found that some genotypes survived at higher population densities relatively better than other genotypes; conversely, certain genotypes showed better survival at lower densities; still other genotypes showed no effect on density.

The purpose of the experiments to be described in this paper is two-fold. First, the effect of population density on the viability of various genotypes will be examined. Second, a study will be made of the effect on the viability of certain genotypes of coexistence with other genotypes at various population densities.

MATERIALS AND METHODS

Twenty-two strains of *Drosophila melanogaster* were used in the course of the experiment. Of these one was a stock of the widely used wild type, Swedish-B, and another was the sex-linked mutant *white.* Nineteen strains homozygous for subvital or semilethal gene complexes were obtained from flies maintained in population cages. These strains were provided through the kindness of Dr. Bruce Wallace. In deriving the strains

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each was made homozygous for a certain second chromosome. In the process of the isolation of these second chromosomes, an estimate of the relative viabilities of the homozygotes from egg to adult stage was obtained. The method of isolation of chromosomes and estimation of the viability of the homozygotes is described by Wallace (1952). Finally a stock was prepared by mating males from six of the homozygous strains with females of six others. The F_2 and later generations from this cross are referred to as "random heterozygotes." All stocks were maintained by mass culture and received identical treatment as far as could be determined.

Flies of the desired genotype were allowed to oviposit on the usual cream of wheat-molasses medium seeded with a yeast suspension. The medium was spread on the surface of a glass plate 12 cm. × 4 cm. and this together with about fifty flies was placed in a bottle with a screw cap.

Larval viability tests were carried out in 25 mm. × 95 mm. shell vials containing 4 cc. of Kalmus' (1943) medium. To insure uniform consistency of the substrate, preparation of the medium was carried out below 70° C. This avoids hydrolysis of the agar by the acid medium. 14 mg. of fresh yeast was added to each tube in 0.1 cc. of water just prior to introduction of the larvae.

All stock cultures and all experimental tubes were maintained at 25 ± 0.5° C.

Egg Hatchability

To determine egg hatchability flies were allowed to oviposit for 18 hours. After this time the oviposition plates were removed and the eggs counted. The plates were then kept without flies for an additional 24 hours after which the number of unhatched eggs was determined. Table 1 shows the total number of eggs counted for each strain and the proportion of these which hatched. In several cases the eggs were collected on two consecutive days although most of the results represent a single day's egg laying. As it was observed that there was no great difference in egg hatchability from one day to the next, no separate record was kept for each day's results with the exception of one case. Table 1 shows two values for the hatchability of eggs of the Swedish-B strain. These values were determined about two generations apart. A chi-square test of homogeneity between these two replications gives a chi-square value of 0.82 with one degree of freedom corresponding to a probability of 0.4. In contrast, a heterogeneity test between strains gave a chi-square of 2,138 with 21 degrees of freedom, corresponding to a probability of very much less than 0.0001. It is quite possible that Swedish-B is less subject to changes in technique than other strains. No experimental check of this possibility was made.

Table 1. *Egg-hatchability*

Strain	No. of eggs	Proportion hatched
1	523	.109
11	500	.830
18	617	.757
22	516	.748
24	566	.563
25	643	.717
28	525	.661
33	517	.803
34	522	.805
41	390	.410
45	524	.693
46	586	.456
47	510	.665
48	658	.913
50	559	.653
54	583	.818
62	521	.823
67	545	.837
74	387	.834
SWB	455	.952
	365	.937
W	535	.923
Rand. Het.	717	.946

Larval Viability

In experiments on larval viability, oviposition took place over a 24 hour period.

TABLE 2. *Larval viability: No. of vials in each series tested*

Series	Total larval density per vial					
	1	2	4	8	20	40
Pure						
A	40	20	10	10	10	10
B	—	20	10	10	10	10
Mixed	—	40	20	10	10	10

The plates were then removed and early first instar larvae were transferred to the experimental tubes with a dissection needle. Table 2 shows the number of larvae placed in each vial and number of replications of each density in the various experiments.

"Pure" cultures are those in which only larvae of the particular strain under investigation were placed in a tube. "Mixed" cultures, on the other hand, contained equal numbers of larvae of the tested strain and of the mutant *white*. Strains were not tested simultaneously and the mixed culture experiments were carried out approximately three generations after the pure culture tests. In order to evaluate the effects of possible experimental errors, the pure culture tests were repeated approximately six generations after the first series. Series A and B in table 2 designate these two repetitions of the pure culture experiments.

The results of the larval viability tests are summarized in tables 3 and 4. The results given represent the proportion of those larvae introduced into the vials which successfully hatched as adults. The values in table 3 are means of pure culture series A and B lumped together. In table 4 the viability of the tested strains in mixed culture is given, together with the corresponding viability of *white* in the same vials.

1. *Pure Culture Experiments*

The first question to be asked is whether a given strain differs in its viability from

TABLE 3. *Larval viability in pure cultures*

Strain	Total larval density per vial						
	1	2	4	8	20	40	χ^2
1	.475	.633	.800	.675	.683	.302	323.9
11	.775	.825	.838	.819	.880	.579	146.9
18	.675	.850	.850	.700	.330	.048	540.3
22	.800	.782	.731	.752	.725	.604	35.5
24	.897	.944	.916	.829	.863	.758	38.9
25	.750	.856	.803	.800	.845	.626	82.8
28	.625	.781	.803	.729	.770	.750	8.4
33	.800	.842	.686	.914	.795	.512	168.4
34	.800	.863	.745	.817	.893	.876	14.6
41	.800	.775	.850	.844	.870	.600	122.0
45	.800	.832	.851	.862	.813	.881	10.8
46	.875	.875	.775	.800	.770	.697	23.5
47	.775	.855	.895	.908	.870	.456	301.2
48	.950	.900	.850	.912	.840	.747	40.9
50	.900	.925	.900	.937	.785	.695	68.2
54	.825	.894	.846	.835	.753	.576	105.5
62	.875	.838	.847	.864	.840	.857	1.2
67	.900	.825	.925	.700	.865	.425	65.3
74	.850	.812	.844	.808	.780	.702	26.0
SWB	.950	.888	.908	.914	.875	.689	92.9
W	.725	.700	.625	.630	.600	.481	34.7
Random Heter.	.900	.925	.928	.934	.910	.902	2.4
Mean	.806	.837	.828	.817	.789	.626	

TABLE 4. *Larval viability in mixed culture*
(T = tested genotype; W = white)

	Total larval density per vial									
	2		4		8		20		40	
Strain	T	W	T	W	T	W	T	W	T	W
1	.675	.700	.700	.600	.525	.675	.500	.610	.210	.550
11	.825	.625	.825	.525	.875	.650	.900	.360	.955	.415
18	.725	.700	.825	.650	.750	.750	.720	.630	.160	.690
22	.825	.625	.925	.800	.675	.550	.740	.600	.655	.585
24	.513	.718	.725	.675	.875	.675	.890	.610	.805	.685
25	.743	.667	.775	.400	.800	.425	.800	.450	.600	.503
28	.675	.600	.625	.575	.500	.700	.560	.690	.625	.620
33	.750	.800	.850	.625	.750	.600	.850	.670	.230	.635
34	.710	.710	.875	.425	.800	.600	.830	.650	.680	.550
41	.875	.475	.973	.605	.925	.450	.860	.590	.735	.570
45	.925	.500	.850	.400	.900	.400	.890	.460	.600	.560
46	.900	.675	.650	.650	.750	.525	.680	.580	.665	.590
47	.825	.775	.950	.725	.950	.850	.960	.670	.840	.725
48	.700	.725	.875	.650	.800	.525	.880	.600	.825	.510
50	.925	.625	.900	.325	.720	.600	.900	.590	.685	.550
54	.775	.700	.675	.575	.700	.700	.710	.550	.515	.530
62	.763	.736	.775	.525	.675	.675	.790	.670	.690	.665
67	.975	.650	.900	.700	.925	.625	.930	.710	.611	.633
74	.675	.750	.800	.850	.725	.725	.700	.690	.595	.725
SWB	.775	.750	.800	.525	.850	.625	.870	.580	.795	.565
Rand. Het.	.925	.650	.900	.675	.825	.800	.790	.710	.750	.515
Mean	.785	.674	.818	.594	.776	.625	.798	.603	.629	.589

one density to another. To determine this, a test of homogeneity between densities was made for each strain separately. The results of these tests are given in the last column of table 3. All of these chi-square values have 5 degrees of freedom. Of the twenty-two strains tested only five show probabilities greater than 0.001. Two strains, 62 and *random heterozygotes,* show very high probabilities of 0.92 and 0.72, respectively. These strains seem completely unaffected in their viabilities over the range of densities tested. It should be pointed out that these chi-square values have meaning only when compared with the variance from vial to vial for a given strain at a given density. The usual method of treating the data would be to calculate the total chi-square between vials and compare this with the chi-square values shown in table 3. This is not possible here because in vials with low population density the vial to vial variance is not even approximately distributed as chi-square. In the case of densities of one larva per vial, for example, the variance has no distribution but is algebraically equal to the sampling variance. In vials with two, four and eight larvae, the variance is less restricted but still cannot be considered to have a chi-square distribution. In order to surmount this difficulty a simple non-parametric test of the following sort was used. Whatever the distribution of the variances from vial to vial, the ratio of this variance to the binomial sampling variance should be close to unity if the vials are homogeneous. This ratio was calculated for all strains at all population densities except that of one larva per vial. Of 110 such ratios, 61 were greater than unity compared with an expected number of approximately 50. This corresponds to a probability of 0.04. Moreover, with the exception of a single value of 6.3 and one of 0.26 all of the ratios lay between 2.3 and 0.45. Such a test, although not

exact, has the advantage of being independent of the number of larvae in each vial. It shows that the large chi-squares in table 3 cannot be due to heterogeneity between vials. The conclusion is justified, then, that there is an effect of density on most of the strains tested and that at least two strains, *62* and *random heterozygotes,* showed viabilities independent of density over the range tested.

An examination of only the chi-square values for heterogeneity from density to density does not show the pattern of change of viability. This can be seen by inspection of the individual values in table 3. The clearest change in viability for most strains is at a density of 40 larvae per vial. In all but five strains the lowest viability is at this density. Among these five exceptional cases only one has a significant heterogeneity chi-square. This lowered viability at high density may be regarded as a result of a lack of sufficient food and so hardly unexpected. There must clearly be some density at which resources are in such short supply that a lowered larval survival appears. On the basis of this simple explanation it might be expected that a density of one larva per vial should give the highest viability, or at least a value not significantly lower than at greater densities. It turns out that only in seven cases, one of which does not have a significant chi-square, is one larva per vial the optimal density. In eight strains, two of which are not significantly heterogeneous, a density of one larva per vial shows either the lowest or next to the lowest viability. For the majority of strains, then, the optimal density is an intermediate one. This effect is reflected in the grand means shown at the bottom of table 3. These means cannot be compared statistically because of the great variance from strain to strain, but the trend is clear. Intermediate densities are optimal while viability is lowered at the highest and lowest population densities.

As has been pointed out, all strains do not react alike. Thus, strains 28, 62 and the *random heterozygotes* show no sig-

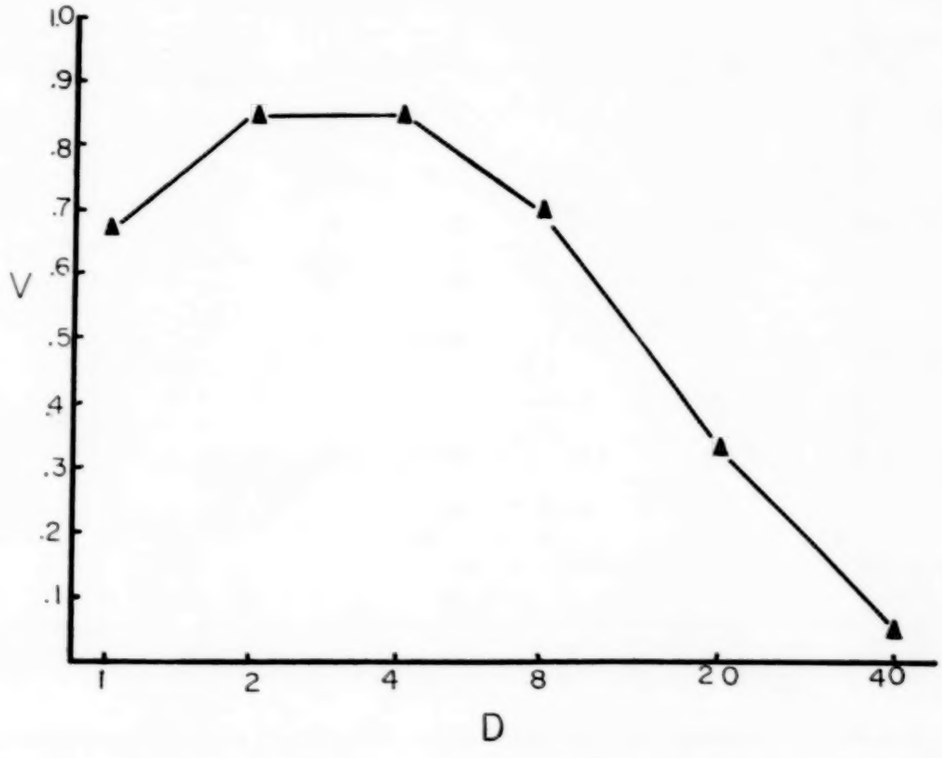

FIG. 1. The viability of homozygote 18 in pure culture at various densities. Viability (V) is plotted on the ordinate and density (D) on the abscissa.

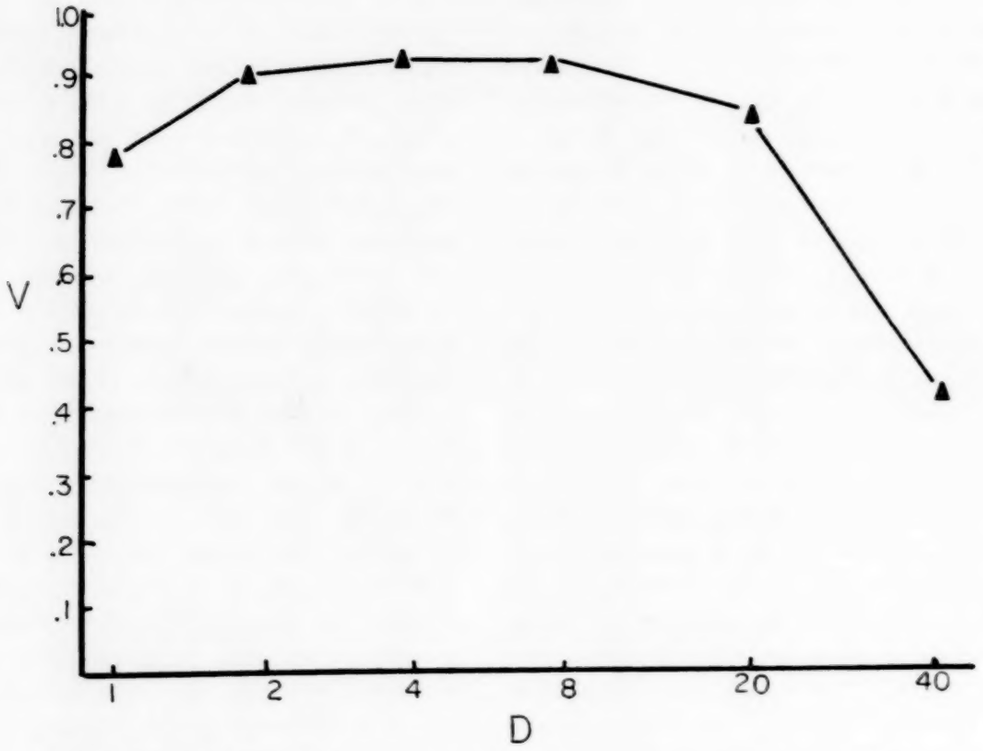

FIG. 2. The viability of homozygote 47 in pure culture at various densities.

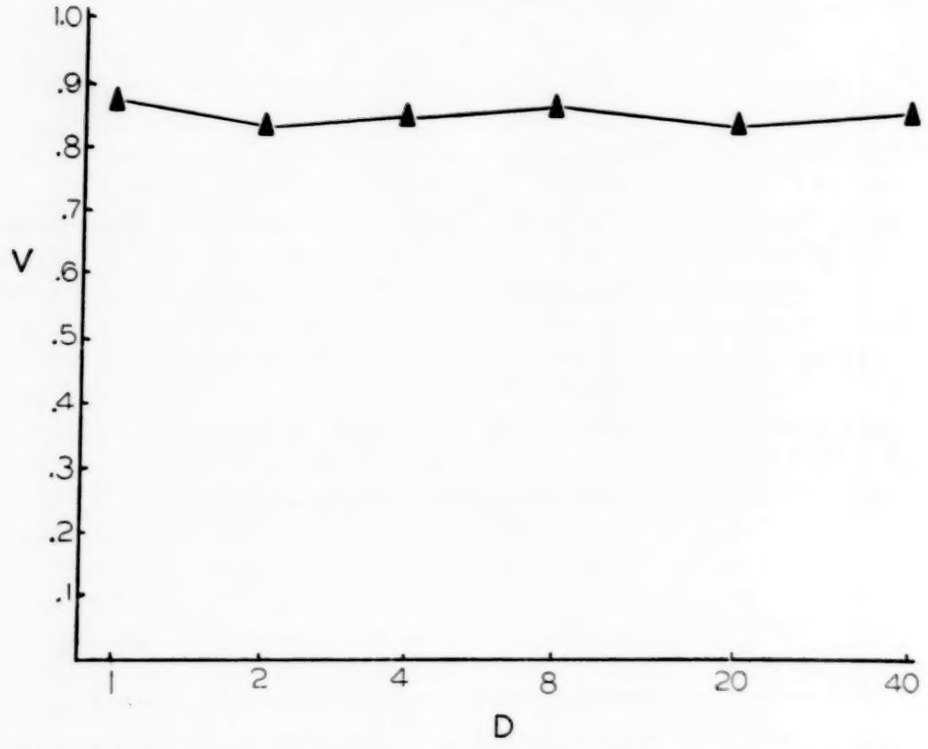

FIG. 3. The viability of homozygote 62 in pure culture at various densities.

nificant differences in viability from one density to another. Strain 22 and ***white*** show a steady decrease in viability with increasing density, the lowest density having the highest viability. Finally strain 45 shows an increase in viability with increasing density, but this is on the borderline of significance ($P = 0.055$).

The difference in reaction to varying population density on the part of different strains is shown graphically in figures 1, 2 and 3. Figure 1 shows the great sensitivity of strain 18 to low and high population densities. Figure 2 shows a more typical reaction, in this case that of strain 47. Finally, an example showing no change with density is shown in figure 3. The strain shown is 62 which yields the lowest chi-square value in table 3.

A second comparison which can be made concerns the differences between homozygotes at the same density. In comparing strains it is necessary to eliminate variability due to the fact that the strains were not tested simultaneously. As series A and B were made about six generations apart, a test of homogeneity between these series provides an estimate of the variance due to lack of simultaneity in the experiments. The chi-square values are shown in the first line of table 5. The second line of table 5 shows the values of chi-square for the test of homogeneity between strains. It is quite clear from a comparison of the two sets of values that the strains are significantly different from each other at all densities. The discrepancies between homozygotes may be looked at in another way. If we compare only the highest viabilities of each of the strains, irrespective of the particular population density at which they occur, a homogeneity test gives a chi-square of 46.4 with 21 degrees of freedom. This corresponds to a probability of 0.0012. It is apparent, then,

TABLE 5. *Chi-squares and correlations for different densities*

		Density of larvae per vial					
		1	2	4	8	20	40
χ^2 between series A and B	χ^2	—	28.83	16.75	26.41	28.39	34.28
	d.f.	—	21	21	21	21	21
	P	—	.12	.70	.19	.13	.035
χ^2 between strains of pure culture	χ^2	62.22	66.70	72.33	192.08	801.47	2,942.14
	d.f.	21	21	21	21	21	21
	P	<.001	<.001	<.001	<.001	<.001	<.001
χ^2 between strains in mixed culture	χ^2	—	57.29	52.84	67.38	178.55	733.70
	d.f.	—	20	20	20	20	20
	P	—	<.001	<.001	<.001	<.001	<.001
χ^2 between pure and mixed culture strain by strain	χ^2	—	76.27	43.23	69.49	118.56	529.06
	d.f.	—	21	21	21	21	21
	P	—	<.001	.003	<.001	<.001	<.001
χ^2 between whites in mixed culture	χ^2	—	22.24	53.67	46.80	62.77	197.95
	d.f.	—	18	18	18	18	18
	P	—	.22	<.001	<.001	<.001	<.001
Correlation between strain and white for vials	r	—	−.068	+.075	+.241	−.021	−.331
	s.e.	—	.036	.073	.073	.073	.073
Correlation between strain and white for strain means	r	—	−.473	+.095	−.092	−.099	−.176
	s.e.	—	.178	.227	.227	.227	.227

TABLE 6. *Analysis of variance on values in table 3*

	Sum of squares	D.F.	σ^2	F	P
Density	692,365	5	138,473	30.88	<.001
Strain	985,627	21	46,935	10.46	<.001
Interaction	470,679	105	4,483	1.97	<.005
Error	250,780	110	2,280	—	
Total	2,399,451	241	—	—	—

that the homozygotes differ even at their optimal densities.

The comparison discussed may be made in still another way. Table 6 shows the results of an analysis of variance on the values in table 3. The F values are calculated on a components of variance model. The estimate of the error variance is derived from the differences between days rather than between vials for the reasons already discussed. The analysis of variance shows as did the χ^2 analysis that there is a significant effect due both to strains and density. Moreover, the analysis of variance shows a significant interaction between density and strain effects. This is a statistical confirmation of the observed differences in the *pattern* as well as the levels of viability with changing density. These differences in pattern are shown in figures 1, 2 and 3.

2. *Mixed Culture Experiments*

The mixed culture experiments were made in order to test whether the viability of a genotype may be affected by the presence of another genotype in the environment.

A homogeneity test was performed on the values in table 4 to determine whether at a given density there were differences between homozygotes as in the case of the pure cultures. The chi-square values are shown in the third line of table 5. As for the pure culture tests, there is significant heterogeneity at all densities. It is interesting to note that the chi-square values for the mixed cultures are consistently lower than those for pure cultures. No comparison is possible, of course, at a density of one larva per vial. The comparisons to be made between pure and mixed cultures are between cultures having the same *total* larval density. Thus, mixed cultures containing 20 white larvae and 20 of the tested genotype are compared with pure cultures containing 40 of the tested genotype. Clearly other comparisons are possible, but that based on total density seems the simplest and most direct. The fourth line of table 5 shows the chi-square values obtained when the pure and mixed cultures are compared. Each strain was compared separately at each density and the chi-square values summed over all strains. There is a significant difference between mixed and pure cultures at every density. This difference is not systematic however. A comparison of the grand means at bottom of tables 3 and 4 shows that on the average there is no tendency for homozygotes to be improved or debilitated in mixed as opposed to pure culture. The grand means are, as a matter of fact, surprisingly similar, in view of the large strain to strain differences shown by the chi-squares between pure and mixed cultures.

Some strains show a marked improvement in mixed culture at high densities. Homozygotes 11, 18, 47, and 67 all show striking increases in viability at a density of 40 larvae per vial. Most impressive is the improvement of strain 11 from a viability of 0.579 in pure culture to a value of 0.955 in mixed culture. Other strains, on the other hand, are depressed in their viability in mixed as opposed to pure culture. Of considerable interest is the progressive drop in viability with

increasing density of the random heterozygotes in mixed culture until at a density of 40 larvae per vial the viability has dropped from 0.902 in pure culture to 0.750 in mixed culture. Other strains showing marked drops in viability at high densities are homozygotes 33, 34 and 45. Nearly all homozygotes show a change from mixed to pure culture at some density. At the 0.01 level of significance, only strains 1, 25, 45, 46, and 54 do not show a significant change at any density.

The data in table 4 may be looked at from a different point of view. It is possible to compare the performance of *white* larvae when coexisting with various other genotypes. Line 5 in table 5 gives the chi-square values for a test of homogeneity of *white* when interacting with different strains. With the exception of the lowest population density, the viability of *white* larvae varies significantly from experiment to experiment. That this cannot be explained by day to day changes in culture conditions has already been demonstrated. The conclusion to be reached from this result is that not only does a given genotype have a different viability in a mixed population from that in a pure population, but that mixtures with different genotypes affect it differently.

As it has been shown that both genotypes in mixed culture are affected by this mixture, it is of interest to see whether these effects have some quantitative relation to each other. To explore this possibility, correlation coefficients were calculated between the viability of white larvae and the viability of the strains with which white was mixed. The first correlation tested is between the numbers of white and wild type larvae surviving in each vial of the mixed culture experiments. The second correlation is between the mean number of white larvae and the mean number of wild type larvae in each

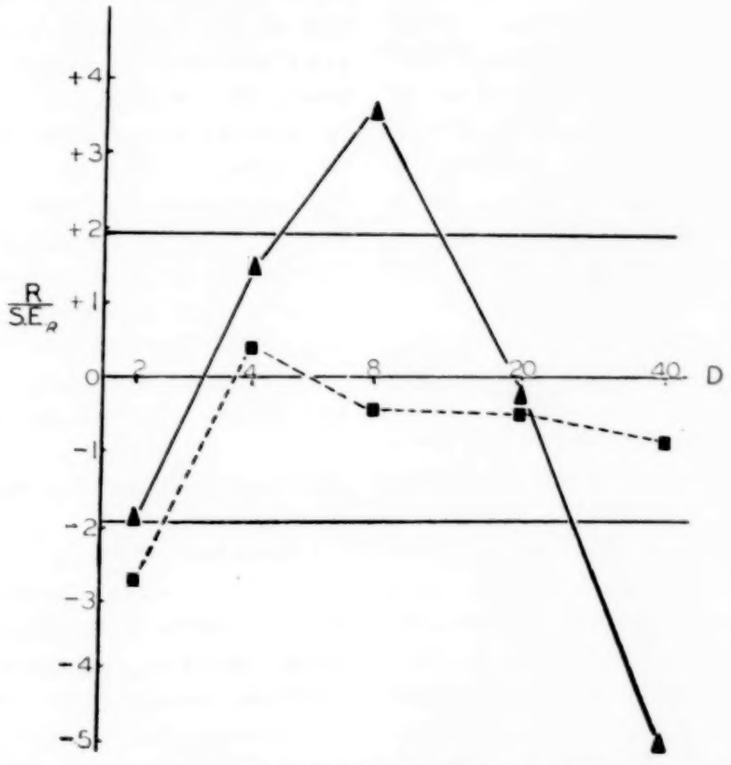

FIG. 4. The correlation between the viabilities of wild type and *white* at various densities. (▲———▲) vial to vial correlations within strains. (■— — — —■) correlations between means. The values on the ordinate are the ratio of the correlation coefficient to the standard error.

strain tested. The within strain variances and covariances were calculated separately for each strain. When these values were added over the strains the total variance and covariance were used to find the correlation coefficient. The results are shown in lines 6 and 7, respectively, of table 5. Figure 4 shows this information graphically. The ordinate represents the ratio of the correlation coefficient to its standard error. This ratio has been plotted since it reduces the coefficients to a comparable scale. Population density is plotted on the abscissa. The heavy horizontal lines represent the 0.05 level of significance for the ratios. Any point falling between them reflects a correlation not significantly different from zero.

Both the correlation in vials and in means show the same trend. There is a negative correlation at the lowest and highest densities, with a positive correlation at some intermediate density. What is interesting here is the rough correspondence to the change in viability with density. Just as the correlation coefficient is negative at extremely high and extremely low densities and positive in intermediate densities, so the viability is low at the extremes with an optimum at some intermediate point. As has been pointed out, this trend in viability is not invariable, but the majority of strains do exhibit it.

Competition and Natural Selection

In discussing the results of the foregoing experiments it is essential that certain concepts and words be unambiguously defined. Darwin, in discussing the "struggle for existence," used this term for two different processes. Thus, he writes, "Two canine animals, in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought. . . ." Although the term competition has replaced Darwin's "struggle for existence," it is often used in the same context. Competition here will be used only in Darwin's first sense. That is, organisms will be said to *compete* if at the same time and in the same place they are using a resource which is in short supply. Organisms on which some factor of the environment impinges irrespective of the number of other organisms subject to the same environment, will be said to *depend* on that factor. In this way a developing frog egg may be said to depend on the temperature of the environment. Finally, organisms *facilitate* each other if their presence in an environment is mutually beneficial. All three of these processes lead to natural selection and thus to evolution, which is to say, "a change in the genetic composition of populations."

The results of the experiments on pure cultures show clearly that all three of these processes play a role in determining the viabilities of the genotypes investigated. The large differences in the viabilities of the strains at high population densities can be interpreted only as a result of the differential response of these genotypes to competition. The fact that nearly all genotypes show a marked drop in survival at a density of 40 larvae per vial indicates that some resource such as food, moisture or space is in insufficient supply. It is not surprising that large differences exist between the viabilities of genotypes under crowded conditions. The population cage technique which has been used so extensively by Dobzhansky and his co-workers to demonstrate differences in the adaptive properties of genotypes, represents a high level of competition.

Of somewhat more interest is the evidence of facilitation in the pure cultures. The existence of an optimal density for larval survival, below which viability is lowered, seems a clear demonstration of a facilitation effect. If any resource is in short supply in the lowest densities, which is present in intermediate densities, this resource must be one which is supplied by the organisms themselves. The appear-

ance of facilitation is not altogether surprising in view of the many observations of the same phenomenon in species populations of a great variety of organisms. This work which has been thoroughly reviewed by Andrewartha and Birch (1954) and Allee (1951) need not be considered in detail. However, such an effect has not been previously described for genotypes within a species.

Of considerable interest from the point of view of evolutionary dynamics is the observation that genotypes differ in their viabilities at their optimal densities. It might have been argued that the differences observed between genotypes at each density were due simply to a displacement of the optimum along the density scale. This is not the case. It must be concluded that various genotypes possess some component of adaptive value which is not a function of density. This is what is meant by natural selection due to dependence on environmental factors. The clearest example of a genotype whose adaptive value is not a function of competition or facilitation is that of a lethal which dies as a result of a metabolic abnormality. Such lethals die independently of the fate of other genotypes in the environment. The results of the egg hatchability tests also give examples of density independent mortality. It must be supposed that the failure of an egg to hatch is not a result of the success or failure of hatching of other eggs, but due to the dependence of the genotype on some other factor. There is no implication here that such organisms would die in all environments. What is implied is that the life or death of the embryo is not the result of the action of the other organisms developing around it.

These considerations have a bearing on evolution in expanding populations. When a population occupies a new ecological niche in which resources are in ample supply, competition is relaxed and for a short period may even be lacking completely. Nevertheless natural selection will still continue to operate since genotypes are seen to differ in their adaptedness to the environment even at their optimal densities. The chi-square values between strains do show the differences in viability are much greater in competitive situations than at optimal densities. The conclusion which can be drawn is that competition is relaxed considerably in an expanding population, but that natural selection still goes on, albeit at a lower rate.

The Interaction of Genotypes

The ideal method of studying the dynamics of evolutionary change is to observe the alteration in the genetic structure of a population over time. This method of attack is limited chiefly to populations containing genotypes which are morphologically or cytologically distinct. The usual procedure is to isolate genotypes at random from the population and study their adaptive properties separately. From the results of these separate tests, an inference is made about the relative adaptedness of the genotypes when interacting in the population. For example, a series of genotypes isolated from a population may each be allowed to compete with a standard genotype which is morphologically distinguishable. Each of the tested genotypes will then have a viability or adaptive value assigned to it relative to the standard genotype. Thus, some may prove to be lethal, others semilethal, still others subvital and so on. The inference then made is that when these genotypes are interacting in the population they will exhibit approximately the same adaptive values relative to each other as they have when tested separately. In the absence of any evidence to the contrary, this is the assumption which should be made, at least on the grounds of simplicity. The experiments described on the mixed culture tests may supply the evidence to the contrary.

The tests of homogeneity between pure and mixed cultures indicate that at every

density tested, genotypes showed different viabilities when tested with *white* and when tested alone. Had these changes been consistently in one direction, the genotypes would have maintained their same relative positions along the viability scale. Since the changes were not consistent, however, the relative positions of the genotypes are completely altered. For example, strain 11 shows a very much lower viability at a density of 40 larvae per vial than does strain 62, when these genotypes are tested in pure culture. In mixed culture the situation is reversed with strain 11 having a very much higher viability than strain 62. It no longer has meaning to ask whether homozygote 11 is superior or inferior to homozygote 62 even when all the conditions of the environment including population density are specified, unless the genetic structure of the population is also taken into account.

This same phenomenon is seen when the viability of *white* is compared in mixture with different strains. In this case attention is focused on a single strain, *white,* and it is seen to vary significantly in its viability depending upon with which of the strains it is interacting.

These results are paralleled by those of Dobzhansky (1948). He compared the adaptive values of three inversion types from natural populations of *D. pseudoobscura.* These three genotypes designated as ST, CH, and AR were compared in pairs in population cages. In the experiment involving ST and AR, the homozygotes of ST had an adaptive value of 0.80 while those of AR had an adaptive value of 0.50, the heterozygote between them always being assigned the adaptive value 1.0 arbitrarily. When ST and CH were allowed to interact the ST homozygotes again showed an adaptive value of 0.80 while CH homozygotes gave a value of 0.40. On the basis of these two experiments it was expected that when CH and AR were compared directly, AR homozygotes ought to have shown a slight advantage over CH if any at all. When this comparison was made AR homozygotes gave a value of 0.86 while CH had a value of 0.48. The lack of consistency of these three tests was extended in a later experiment of Levene, Pavlovsky, and Dobzhansky (1954) in which all three genotypes were allowed to interact in the same population cage. In this case the AR homozygotes had a much lower adaptive value than CH. The evidence of interaction is quite clear from these results.

The correlation coefficients shown in table 5 also have bearing on the problem of interaction of genotypes. A positive correlation means that the survival of one individual or genotype increases the probability of survival of other individuals or genotypes in the same environment. This is simply another way of stating the principle of facilitation. A negative correlation, conversely, is indicative of a competitive relationship. This competitive relationship is not of the simple type in which the interacting genotypes show viabilities independent of each other. If this were the case there ought to be no correlation at all, the survival of one genotype being statistically independent of the survival of the other. It has been pointed out that the correlation coefficients between *white* and the tested strains follow the same rough relation as do the viabilities. That is, extremely high and low densities produce both low viability and negative correlation, while intermediate densities produce high viability and positive correlation. It is the negative correlation at low, suboptimal densities that is most enlightening. As has also been pointed out, it is not possible to assign a shortage of some resource as the cause of low viability at low densities, unless this resource be produced by the organisms themselves. The negative correlation at these densities seems to point toward a direct interference of one organism with another independent of the amount of natural resources available to them. There are of course any number of explanations which might be given for

such a phenomenon. One possible explanation would be the excretion of a waste product of metabolism by one genotype which is inhibitory to others. Bonner (1950) has reviewed the evidence for such an effect in higher plants. His conclusion is that substances are, in fact, produced by some species which are inhibitory to others. Such might also be the case for genotypes within a species. At low and high densities where conditions are not optimal for either genotype the effects of this inhibition might become manifest. At intermediate densities where viability is at a maximum, the organisms would be less susceptible. At present there is no clear evidence bearing on this point, however.

The Evolutionary Implications of Interaction

Several agencies are known which maintain the genetic variability of a population. The two that have received the greatest attention are a higher adaptive value of heterozygotes and a balance between selection and opposing mutation. Recently Levene (1953) has demonstrated still a third and probably very important mechanism leading to equilibrium of gene frequencies. He has shown that if a population occupies more than one ecological niche and if genotypes differ in their adaptive value from niche to niche, then equilibrium is possible. The precise conditions which must be imposed on the adaptive values are not important to this discussion. What is important is the close relationship between this finding of Levene and the experiments described above. The adaptive value of a genotype varies depending upon the genotypes with which it is interacting. This is simply another way of saying that a genotype has a different adaptive value in differing ecological niches since the organisms present characterize a niche as much as any other environmental factor. In this sense the interaction of genotypes is similar to the problem discussed by Levene. Actually the specific model is quite different. Whereas Levene's model dealt with an ecologically subdivided population with different environments simultaneously present, we must deal with a change in adaptive values over time, which change is a function of the continuously altered genetic structure of the population. A simple case will illustrate the point.

It is easy to show that the change in the frequency of a recessive gene in one generation in a population subject to natural selection, is given by the expression:

$$(1) \qquad \Delta q = \frac{(W-1)q^2(1-q)}{1-(1-W)q^2},$$

where

q = the frequency of the gene in question,
Δq = change in frequency of the gene in one generation,
W = the adaptive value of the homozygote.

With this expression it is possible to predict the frequency of the gene in any future generation and the rate at which the frequency is changing at any particular time. The critical point is that W is usually considered to be a function only of the genotype and the various factors of the environment, but independent of the gene frequency q. It is necessary now to consider the possibility that W is functionally related to q.

The most interesting case is that in which W increases as q decreases. Strain 11 is an example of this since the viability is higher in mixed culture (q =0.5) than in pure culture ($q = 1.0$). For the sake of simplicity we may assume that W is a linear function of q. That is

$$(2) \qquad W = -Aq + B.$$

It is simple to show that an equilibrium at which q neither increases or decreases will occur if

$$(3) \qquad (W-1)q^2(1-q) = 0.$$

This follows directly by putting Δq in equation (1) equal to zero. If W is some constant independent of gene frequency then equation (3) will be satisfied only when q is zero or unity. In other words, the gene is either lost or fixed. On substituting equation (2) in equation (3), however, we see that an alternative solution is that

$$(4) \qquad q = \frac{B - 1}{A}.$$

All values of the constants A and B will not lead to biologically meaningful solutions of equation (4). A biologically meaningful solution is one in which there is a *stable* equilibrium with q lying strictly between zero and unity. In order to have such solutions it is necessary that

$$(5) \qquad A > 0 \quad \text{and} \quad 1 \leqslant B \leqslant A + 1.$$

The requirement that A be greater than zero assures that the line given by equation (2) has a negative slope. That is it assures that the model of decreasing adaptive value with increasing gene frequency is satisfied. The conditions on B given by (5) simply assure that q lies strictly between zero and unity, which are the only realistic bounds for a gene frequency. Should A and B take such values that q in equation (4) becomes less than zero or greater than unity, then the allele in question will be lost or fixed, respectively. The same problem of the adaptive value of a genotype being a function of the gene frequency has been treated by Wright and Dobzhansky (1946) for the more complicated case of no dominance. These authors showed that if W is a linear function of q a sufficient condition for equilibrium is that both homozygotes show facilitation while the heterozygote is exactly intermediate in adaptive value between them.

All the lines of argument presented above bear on a central problem in the study of the genetic structure and evolution of populations. It is the problem of the extent to which a highly organized and integrated supraindividual entity such as a Mendelian population can be understood by a study of its isolated genotypes. It is necessary that some simplifying assumptions be made in the study of a population, but these assumptions must be examined carefully in order to assure that they will give a relatively undistorted picture of the more complex natural system.

Summary

Twenty-two strains of *Drosophila melanogaster* were compared with respect to their larval viabilities. These strains included Swedish-B wild type, the mutant *white,* nineteen strains homozygous for second chromosomes isolated from flies maintained in population cages, and one strain of random heterozygotes from crosses among the homozygous strains.

The larval viabilities were tested at population densities of 1, 2, 4, 8, 20, and 40 larvae per shell vial containing a synthetic medium. Pure culture experiments contained only larvae of the tested genotype, while mixed cultures contained equal numbers of the tested genotype and the mutant *white.*

Most strains showed an optimum viability at intermediate densities although a few showed no change over the range used. The strains differed from each other in viability at all densities. They also differed from each other when compared at their respective optimal densities. In addition there was a change in viability at all densities from mixed to pure culture. Some strains showed an increased viability in mixed culture over that in pure culture while others showed a decrease. This lack of regularity resulted in a change in the relative positions of the homozygotes on the viability scale from pure to mixed culture. Finally a negative correlation between the numbers of wild type and *white* larvae surviving was observed at the highest and lowest densities. The correlation was positive at intermediate optimal densities.

The existence of an optimal intermedi-

ate density indicates some facilitation between individuals of like genotypes. The significant differences between strains when compared at their respective optimal densities point to a component of viability independent of density. This would allow natural selection to work in an expanding population. The increase in viability in mixed culture of some strains shows that a strong facilitation may exist between genotypes. On the other hand the negative correlations at the extreme densities and the lowering of viability in mixed culture for some genotypes show that genotypes may actively interfere with or inhibit one another. The general conclusion is that the viability of a genotype is a function of the other genotypes which coexist with it, the result of any particular combination not being predictable on the basis of the viability of the coexisting genotypes when tested in isolation. That this is general is indicated by the differences in the viability of one genotype (white) when tested with all other genotypes.

It has been shown that facilitation may lead to a stable polymorphism of genotypes.

Acknowledgment

The author owes a great deal to his colleagues and teachers who never tired of bringing their various points of view to bear on the matters discussed here. Most especially is he grateful to Prof. Th. Dobzhansky whose well directed criticism and continuous guidance clarified many problems both theoretical and practical. Prof. Howard Levene was extremely helpful in carefully scrutinizing the manuscript as well as in giving invaluable advice on statistical matters. Dr. Bruce Wallace and his staff have been of immeasurable aid in providing the material for the experiments at the expense of considerable labor and time on their part.

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ECOLOGY AND HYBRIDIZATION IN THE GENUS *BUFO* IN THE MICHIGAN–INDIANA REGION[1]

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INTRODUCTION

Much confusion has existed concerning the relationship to each other of the two forms, *Bufo americanus* (*Bufo terrestris americanus* according to Netting and Goin, 1946) and *Bufo fowleri* (*Bufo woodhousii fowleri* of many authors; see Wright and Wright, 1949). This is well-shown by the number of times that comparisons of the two have appeared in herpetological literature. Such comparisons have been made by Garman (1890), Deckert (1917), Myers (1927), Schmidt (1929), Netting (1929), Myers (1931) and Blair (1941). Of these and other investigators, many (e.g., Deckert, 1917; Myers, 1931; Blair, 1941 and later papers) have found individuals which were difficult to classify, and expressed the opinion, on morphological grounds, that hybridization might occur. Others (e.g., Garman, 1890; Netting, 1929) have stated that the two seem quite distinct and that hybridization is unlikely. Recently Volpe (1952) has presented convincing physiological evidence that hybridization is quite common under natural conditions. Possible hybridization between these and other toads has been indicated by Gaige (1932), Blair (1941, 1942), Netting and Goin (1946), Neill (1949) and Orton (1951).

Blair (1941 *et seq.*) has done extensive work on hybridization of these toads from the point of view of significance in modern theories of speciation and isolation. This work has been briefly summarized and quoted in such modern evolutionary treatises as those of Mayr (1942) and Dobzhansky (1951). Among the chief conclusions of Blair were that these two toads could hybridize and that the hybrids are fertile. Furthermore, he concluded that the calls of the males are of little significance in maintaining isolation (1942), as he concluded also for choice of breeding sites (*ibid*). The principal isolating feature between the two, he concludes in general, is the difference in time of breeding. This difference in breeding season is well-known, and had previously been described, among others, by Myers (1927), Ruthven *et al.* (1928), Schmidt (1929) and by Netting (1929). Concerning the extent of such hybridization, Blair concluded that the hybrids formed a minority group in the region of Bloomington, Indiana, and that they formed smaller breeding populations at a time intermediate between the breeding seasons of the more numerous individuals of the parent species.

Volpe (1952) concerned himself with presenting physiological evidence of the existence of hybrid populations in nature, and minimized the possibility of partial isolating mechanisms existing between the parent forms.

PRELIMINARY LOCAL OBSERVATIONS

The work here reported was done in Cass County, Michigan and in St. Joseph County, Indiana. Cass County lies in the southernmost tier of counties in southwestern Michigan, and is bordered to the

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south in part by St. Joseph County, which is one of the northernmost tier of counties in Indiana. This area thus lies just to the east of the Chicago Area, as defined by Pope (1944), and has been described in detail by us elsewhere (Manion and Cory, 1952). Topographically the area presents an aspect of level to mildly undulating land for the most part, with a few areas of gently rolling to hilly surface. Elevation is from slightly over 700 ft. to about 900 ft. above sea-level.

Vegetational cover of Cass County, as shown by Kenoyer (1933), from a study based on the original land survey, 1826–1832, previous to settlement of the area, was 87% hardwood forest. This was distributed as oak-hickory 59%, and beech-maple 28%. Of the remaining 13%, 9% of the total area was covered by lakes and swamps, and 4% by grassy prairie. At the present time this distribution of land cover is tremendously changed. According to the 1940 census report of the Michigan State Agricultural Bureau, wooded areas comprised at that time only 30,278 acres, or about 9.6% of the total area, and in the 1945 report this figure was reduced to 26,966 acres, or 8.5% of the total area. According to the 1945 report, 273,605 acres, or 86.7% of the total area was in farm and grazing land. Vegetational cover in St. Joseph County, Indiana, is similar.

In the months of April to June, 1950 and 1951, extensive collections were made from large breeding populations of toads at the north edge of St. Joseph Lake on the University of Notre Dame campus, which lies just north of the city of South Bend in St. Joseph County, Indiana. Examination of several hundred individuals gave the impression that most of them showed a combination of characters intermediate between the usual descriptions of the species *Bufo americanus* and *B. fowleri* (e.g., as in Wright and Wright, 1949). Only a small proportion corresponded to typical descriptions of either form. Earlier-breeding individuals appeared more *americanus*-like, while later-breeding individuals were more *fowleri*-like, as indicated by Blair (1941), though we could not agree with his conclusion for the Bloomington, Ind., region, that the hybrids formed a minority group.

During the summer of 1951 amphibian collections were made throughout Cass Co., Michigan. In the course of this collecting, several areas were found from which were taken only individuals corresponding perfectly with typical descriptions of *B. fowleri*. On the other hand, a few areas were found which yielded scattered individuals corresponding to typical descriptions of *B. americanus*. These typical *americanus*-type individuals were also found in the region of Rum Village Park, just south of the city of South Bend, Indiana. Hybrid-appearing individuals were also found in many widely-scattered areas.

Subsequent examination of field notes showed that all areas from which only typical *B. americanus*-like individuals were collected were completely wooded areas; those from which only a typical *B. fowleri*-like individuals were taken were all open fields in which there was generally a pond. Hybrid-appearing individuals were most frequently taken from areas showing mixed wooded and open conditions. Hence the hypothesis was suggested that isolation between these two forms depends on the extent of wooded and open areas in relation to the availability of suitable breeding sites.

Consultation of previous descriptions of the general ecology of these two forms confirmed the credibility of this hypothesis. Many authors (Ruthven, 1905, 1911; Ruthven *et al.*, 1928; Blanchard, 1928; Gloyd, 1932; King, 1939; Bragg, 1940, 1943; Bragg and Smith, 1943; Hatt *et al.*, 1948) had described *B. americanus* as being found in wooded areas. *Bufo fowleri*, however, was frequently described as being found in open areas of one type or another (e.g., Ruthven, 1917; Ruthven *et al.*, 1928; Schmidt, 1929; Schmidt and Necker, 1935; Necker, 1939).

To test this hypothesis, a series of observations was planned for the breeding season of 1952.

Methods

Three sites were chosen to follow breeding populations of toads during the spring of 1952. The first of these was a series of small ponds situated in an extensive completely wooded area at Rum Village Park, South Bend, Indiana. If *B. americanus* is characteristic of wooded areas, then these ponds should show only individuals having characteristics of this form. The pond in which only *B. fowleri* was expected was in a large, open, grassy field at the southern edge of Edwardsburg, Cass Co., Michigan. This is about 12 miles northeast of South Bond. The remaining area selected was the north shore of St. Joseph Lake on the University of Notre Dame campus. Immediately adjoining the lake are small wooded areas, as well as several large open fields.

Observations on the breeding populations in these areas were conducted nightly from the beginning of the breeding season; the three sites were checked continuously from the middle of March, 1952, to be certain that the first toads to appear would be seen. Rather than to collect the toads, it was decided that the breeding populations should be allowed to develop normally. Therefore an index character had to be chosen which would allow accurate quantitative expression and yet which would be possible to measure accurately in the field.

One of the characters mentioned as distinct for these species by practically all describers is the number of warts per darkly-colored dorsal spot. In *B. americanus,* usually 1 or 2 warts per spot have been described, while in *B. fowleri* such spots have generally been described as having from 3 to several warts. Examination of specimens in the collections of the Chicago Museum of Natural History confirmed the usefulness of this character. Accordingly, for each individual, the dark dorsal spot with the greatest number of warts was selected, and the number of warts in this spot was recorded. The mean of this quantity was then calculated for each population, as well as the standard error and the 95% confidence limits of the true mean for graphical representation.

In addition to this character, notes were taken on each specimen regarding the extent of ventral spotting. Arbitrary classes were selected, similar to those used by Blair (1943a), as follows: 1. Completely unmarked. 2. A single pectoral spot only (generally described as typical of *B. fowleri*). 3. Approximately ⅓ spotted. 4. Approximately ½ spotted. 5. Over ½ spotted to completely mottled (generally described as typical of *B. americanus*).

Also noted for each specimen were whether or not the post-orbital branches of the cranial crests contacted the parotoid glands and whether or not the hind tibiae showed large, spiny warts. The first of these characters is described as negative for *B. americanus* and positive for *B. fowleri,* while the other is described as positive for *B. americanus* and negative for *B. fowleri.*

When the breeding populations had reached their peak, series of individuals were taken for preservation and measurement of length. The St. Joseph Lake population measurements were made on animals collected during the 1951 breeding season.

In addition to these measurements, lengths of calls in the three areas were determined by the use of a stop-watch. Eggs were collected and examined, and notes were taken on the behavior of the animals in the field. Notes were also taken on temperatures and their relation to activity of the animals.

Results of Observations

Results of most of the observations which were made are summarized in table 1 and in figure 1. In the Rum Village breeding populations, no significant

changes were found in any character throughout the breeding season, which lasted at this site from April 18 to May 1 in 1952. Therefore the extent of ventral spotting, the condition of the post-orbital cranial crests with respect to contact with the parotoid glands and the presence or absence of tibial spines for all populations at this site are totalled for all dates in table 1. Also, no significant changes in any characters were found in the Edwardsburg breeding population during the extent of the breeding season, which lasted at this site from May 1 to June 5. Hence the characters are totalled for all dates from this site also in table 1. In the St. Joseph Lake area, breeding was found to begin as early as it did in the Rum Village area. At this time, the individuals at St. Joseph Lake were more *americanus*-like than later, yet as a population this group could readily be distinguished from the Rum Village aggregation. As the season progressed, a gradual transition occurred in this population, so that by the latter part of the season they were decidedly *fowleri*-like, though they could still be readily distinguished from the Edwardsburg population. This progression in change of characters in the population is evident in the data of table 1.

Figure 1 shows the results of the observations on the maximum number of warts per single dorsal spot. Vertical lines through each population average indicate the 95% confidence limits of the true mean; if any two of these lines fail to overlap, the indication is thus that the difference between the means is significant. It can be seen from the figure that no significant change in this character occurred throughout the breeding season in the Rum Village populations. The mean here was always close to 2.0. Curve III shows the constancy of this character for the Edwardsburg animals; the mean here was always close to 7.0. The St. Joseph Lake population, however, as shown by Curve II, showed an

TABLE 1. *Numbers of individuals possessing certain morphological characteristics among toads collected from breeding populations as indicated, during the breeding season of 1952*

Symbols used—Ventral spotting: 1. Completely unmarked. 2. Pectoral spot only. 3. Anterior ⅓ spotted. 4. Anterior ½ spotted. 5. Over ½ spotted to completely mottled. Contact of post-orbital cranial crests with parotoid glands: ½ indicates contact on one side only.

	Ventral spotting					Post-orb. contact with parotoid			Tibiae spiny	
	1	2	3	4	5	Yes	No	½	Yes	No
Rum Village										
Apr. 18–May 1	0	0	0	9	120	0	129	0	129	0
St. Jos. Lake										
Apr. 18	0	0	1	0	1	0	2	0	2	0
Apr. 19	0	1	4	9	5	2	16	1	19	0
Apr. 20	0	1	15	14	9	9	27	3	39	0
Apr. 21	1	7	26	18	19	7	52	12	71	0
Apr. 22	0	3	11	13	15	9	27	6	42	0
Apr. 27	0	14	8	6	12	13	26	1	40	0
Apr. 28	1	13	11	6	8	10	26	3	36	3
Apr. 29	0	4	1	1	2	3	4	1	4	4
Apr. 30	0	10	2	5	3	15	3	2	9	11
May 1	0	15	6	1	1	17	4	2	6	17
May 4	0	25	17	13	9	35	21	8	33	31
May 23	0	22	15	14	10	40	10	11	26	35
May 27	0	9	1	0	1	8	3	0	3	8
June 5	0	1	3	1	0	4	1	0	1	4
Edwardsburg										
May 1–June 5	1	105	8	1	1	115	1	0	1	115

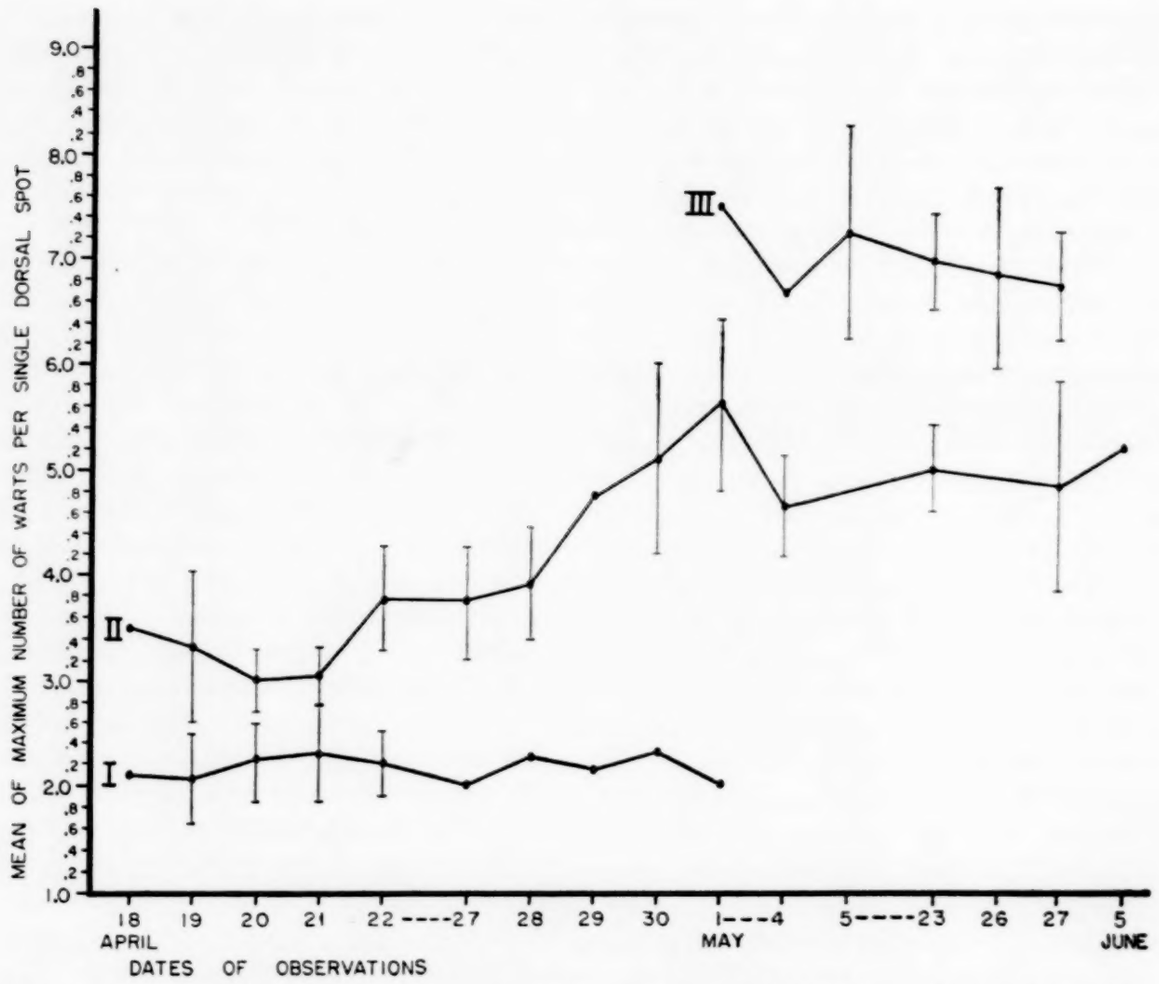

FIG. 1. Averages of the maximum number of warts per single dorsal spot in breeding populations of toads during the breeding season of 1952 near South Bend, Ind., and Edwardsburg, Mich. I. *Bufo americanus* from extensive wooded area at Rum Village Park, South Bend, Ind. II. Hybrid population from lake edge accessible to mixed wooded and open areas on the University of Notre Dame campus. III. *Bufo fowleri* from a pond in a large open field at Edwardsburg. A broken line between two dates indicates that no breeding activity was occurring, due to low night temperatures. A fine vertical line through a population mean indicates the 95% confidence limits of the true mean; this was not indicated when numbers were too small to bring it within reasonable limits. Failure of any two of these to overlap indicates significant difference between the means.

over-all mean close to 3.0 early in the season and an over-all mean close to 5.0 by the end of the season. As indicated by the 95% confidence limits of the means, the St. Joseph Lake population was always significantly higher than the Rum Village populations and significantly lower than the Edwardsburg population whenever numbers were sufficiently large to establish the mean within reasonable limits. Early populations at St. Joseph Lake were significantly lower in this mean than later populations.

Body lengths of 48 males from the Rum Village area averaged 60.18 mm., with a standard error of 0.62 mm. From Edwardsburg, 52 males averaged 55.52 mm., with a standard error of 0.39 mm., indicating a somewhat smaller size for *B. fowleri*. From the St. Joseph Lake area, 150 individuals taken during the early part of the breeding season in 1951, April 27–30, yielded a mean length of 57.84 mm., with a standard error of 0.43 mm., while 110 individuals taken later in the breeding season, May 1–16, had a mean length of 57.30 mm., with a standard error of 0.51 mm. The St.

Joseph Lake animals thus appear to be intermediate in size between the presumed parental forms and to show somewhat of a progression from a larger *americanus*-like size to a smaller *fowleri*-like size as the season progresses.

Results of other observations were as follows:

Eggs: Eggs of *B. americanus* were found to be laid in strings having a double tubular membrane and partitions between adjacent eggs, which agrees with published descriptions (e.g., Wright and Wright, 1949). Those of *B. fowleri* have only a single tubular membrane and no partitions between eggs. Eggs were taken from St. Joseph Lake which showed all degrees of intermediacy. Some were like typical eggs of the parental forms. Most, however, had a double tubular membrane with no partitions between eggs, while some had a double tubular membrane and an occasional partition between adjacent eggs.

Length of Calls: Bufo americanus has always been described as having a call which is a long musical trill, while *B. fowleri* has been described as having a short, harsh call. Calls heard at the Rum Village site were of the former type. Ten of them were timed, and averaged 9.4 seconds in duration. Calls at the Edwardsburg area were so short that accurate timing was impossible. Most calls were approximately 1 second or less in duration, so that the mean would be less than 1 second. Most of the calls heard at St. Joseph Lake were intermediate in nature, agreeing well with what Volpe (1952) calls peculiar "buzz saw" trills. At the beginning of the 1952 breeding season, from April 18 to April 22, the mean duration of 33 calls was 6.3 seconds. From April 27 to April 30, the mean duration of 23 calls was 4.0 seconds. For the rest of the breeding season, the mean of 18 timed calls was 2.8 seconds.

Temperature Thresholds: The establishment of precise temperature thresholds for reproductive activity under natural conditions is very difficult due to the complexity of inter-action of air and water temperatures. The males are generally partly submerged when calling, and so are exposed to conditions in both situations. Most of our observations involved air temperatures. At Rum Village, the temperature threshold for calling was found to be close to 60° F. (16.5° C.). Very few calls were heard at a temperature as low as 57° F. Good choruses were heard at temperatures above 60° F. At Edwardsburg, calling did not begin until May 1, when the night temperature was 68° F. when observations were made. Good choruses were heard only at temperatures above 70° F. (21° C.). On one occasion a fairly good chorus was heard at an air temperature of 66° F. On this occasion, however, the air was quite still, and the water was at a temperature of about 74° F., so that the air temperatures where the individual animals were located were probably higher than 66° F. These observations would place the threshold for this population at about 68–70° F. (20–21° C.). At St. Joseph Lake early season individuals exhibited a threshold close to that of the Rum Village group. Fairly good choruses were heard at about 60° F. and above. By May this had changed, so that on the night of May 3, at a temperature of 60° F. nothing was heard, although good choruses resumed on subsequent nights at higher temperatures.

Behavior: This is difficult to evaluate quantitatively. However, purely descriptive observations fit well with other findings. Individuals at the Rum Village area were very active. There was a great deal of general scrambling about, with males clasping one another and quickly releasing in response to the warning vibration (Aronson, 1944). Disturbance of the water, as for example by walking through it, attracted the animals, and many would usually swim towards the source of the disturbance. At Edwardsburg, the animals were much more spread out around the edge of the pond. Most individuals were hidden among clumps

of grass and sedges, and remained quiet and motionless when approached. At St. Joseph Lake, early in the season the individuals were mostly found in a relatively small area; disturbance of the water frequently caused them to turn, so that they were facing the source of the disturbance. They were never as active, however, as the Rum Village animals. Later in the season, individuals were much more scattered along the lake edge, and a large proportion were hidden while calling.

Discussion

All the available evidence, whether morphological, physiological or behavioristic, points to the conclusion that the St. Joseph Lake toads form a hybrid population, as was concluded by Volpe (1952) for the Westwood, Now Jersey, population studied by him. That this population is best considered hybrid at all times in the breeding season is indicated, among other features, by the significant difference between this population in the number of warts per dorsal spot and the "pure" *B. americanus* and *B. fowleri* populations of the Rum Village and Edwardsburg sites respectively at all times in the season.

Blair (1941, 1942) discussed possible isolating mechanisms between these two forms. He found that response to calls, breeding site selection and difference in breeding season were all more or less inadequate as isolating mechanisms, though he seemed to lay greatest stress on the difference in breeding season as resulting in partial isolation.

In 1952, both of these toads were calling locally on May 1, this date representing the date of the last calls of *B. americanus* and the date of the first calls of *B. fowleri*. With the data for temperature thresholds, it is evident that these two breeding seasons could be completely separate or could overlap considerably. A late spring with sudden change to evening temperatures above 70° F. would presumably bring both forms out. On the other hand, a long series of evenings with temperatures slightly above 60° F. would allow *B. americanus* to complete its breeding well before *B. fowleri* would begin.

The intermediate temperature thresholds of the hybrid populations, once such were formed, would produce, as happened locally in 1952, a continuous breeding season from early in *B. americanus* season to late in the *B. fowleri* season. Hence, once a hybrid population is formed, this seasonal isolation becomes as ineffective as response to calls or choice of breeding sites. In regard to the first date of breeding activity among toads in 1952, it is highly interesting that our first date, April 18, for the Cass County, Michigan area is the same as Volpe's (1952) first date for the New City, New York and Montvale, New Jersey areas. It is also interesting to note that the lowest air temperature at which we found breeding activity, 57° F. (14° C.) was the same as Volpe's value (14° C.) for the minimum water temperature which would allow such activity.

We agree with Volpe that these toads may be found breeding in any of a variety of aquatic situations. We have found eggs of *B. americanus,* for example, in a pond of about 20 ft. in length, 2 to 3 ft. in width and a few inches deep at Rum Village, while on the other hand we have found them in an extensive *Typha*-filled swamp of many acres extent in a wooded area near Eagle Lake, Cass County, Michigan, and Volpe reports them from a number of different situations.

Locally, at least, the correlation is remarkable between the appearance of the individuals and the type of non-breeding habitat. Typical *americanus*-like individuals have been found consistently in extensively wooded areas, typical *fowleri*-like individuals in open, grassy areas, and intermediate types in areas of mixed vegetation. This, we believe, is the determining factor in establishing the characteristics of the populations.

From table 1, it is evident that lower numbers of individuals were present at the middle of the hybrid breeding season than earlier or later. This may represent a characteristic feature in the breeding pattern of the hybrid population, or it may have been due to low temperatures at this time. On April 28 the temperature at about 10:00 P.M., Central Daylight-Saving Time, was 59° F.; on April 29, 57° F.; on April 30, 61° F.; on May 1, 65° F. These are the dates of mid-season low numbers, and it must be kept in mind that at this time the temperature threshold in the population was rising. On May 4, when the temperature at the same time of night was 74° F., numbers of animals were again high.

On the other hand, low mid-season numbers of strictly intermediate individuals might be due to the action of natural selection in the non-breeding habitat. If a large wooded area and a large open field were located near the same breeding pond, then presumably strictly intermediate individuals would be at a disadvantage in either area. However, a locality of well-intermingled small wooded and small open areas might be characterized by more intermediate individuals. In other words, as Volpe (*op cit.*) has suggested, new adaptive peaks may be realized from hybrid combinations. Moreover, the action of natural selection in the non-breeding habitat areas appears to be very severe. It is difficult to imagine that no *B. fowleri* migrate into wooded areas or that no *B. americanus* move into open spaces. In fact, on May 1 one typical *B. americanus* was found at the Edwardsburg field (see characteristics in table 1). Yet the apparent purity of the two forms in their typical habitat areas is remarkable.

Another possible contributing cause to the presence of two more or less distinct groups in hybrid populations would be the migration of pure types from neighboring areas of a strictly wooded or strictly open character, followed by backcrossing with the hybrids.

Some evidence is available that the characteristics of the hybrid populations may be determined by the particular conditions of their habitat areas. Approximately 1,200 to 1,500 ft. from St. Joseph Lake is a rather large swampy area, separated from the lake area by a road and several buildings. At this location the surroundings are more wooded than at the lake. On a few occasions after May 1, temperatures for the lake population were slightly low for calling; individuals in the other area, however, were calling. Throughout the breeding season the calls in the swampy area were more *americanus*-like than at the lake, and the former population finished its breeding activity before the latter. Close check and detailed observations were not kept on the swamp area, however, so that exact comparison cannot be made.

How these two forms became as divergent as they have, in spite of their extensive hybridization, presents a theoretically difficult problem. Considerable light is shed upon this matter, however, by the report of Kenoyer (1933). As brought out in an earlier section of the present paper, he showed that previous to deforestation in Cass County, Michigan, which began about 1835, the county had about 87% of its area in hardwood forest, and only about 4% in grassy prairie. As has been seen, this extensive wooded area was reduced to only about 8.5% of the county's area in 1945, and this, of course, is in the form of small scattered wooded sections in open farming land.

Possibly *B. fowleri* was originally geographically isolated from *B. americanus*, the former to the west in open country. Deforestation and clearing of the land would then allow eastward spreading of *B. fowleri*. The breaking-up of the wooded areas would tremendously increase the number of bodies of water available to animals from ecologically mixed areas, and hybridization would proceed at a tremendously increased rate.

The question may be brought up as to

the relative taxonomic status of these two forms. At present they are considered specifically distinct by all herpetologists. Were the two forms to be geographically separated, with the same degree of hybridization at the line of contact, they would probably be assigned subspecific status. The present situation, at least locally, best corresponds to that described by Mayr (1942), under classification 3 (p. 263), when geographic isolation breaks down: "The two populations have acquired different habitat preferences during their isolation, but not reproductive isolation. This results in a curious interlacing of ranges, with hybridization at the borders of habitats." Carter (1951), commenting on this situation, refers to the populations in such cases as subspecies.

Designation of these forms as ecological subspecies is not formally suggested here, as the situation should be investigated at widely-separated areas throughout their sympatric range.

Summary

1. Observations made at three ecologically characteristic sites in the Michigan-Indiana region confirmed the hypothesis originally formulated from distributional data that *Bufo americanus,* as such, is found in wooded areas containing breeding sites, that *B. fowleri,* as such, is found in open areas containing breeding sites, and that ecologically mixed areas support hybrid populations.

2. The hybrid population studied was at all times significantly different from either parent form, though it showed a progression from early season predominantly *americanus*-like individuals to late season predominantly *fowleri*-like individuals.

3. *Bufo americanus* shows reproductive activity at temperatures of about 60° F. and above, while the threshold in *B. fowleri* is slightly less than 70° F. Hybrids show intermediate thresholds, with a seasonal progression as for morphological characteristics. Normal progression of seasonal temperatures causes *B. americanus* to breed before *B. fowleri,* though this is subject to considerable variation, depending on weather conditions, and the seasons may overlap locally.

4. Hybrid groups form continuously-breeding populations, except on nights of low temperature, from the beginning of the *B. americanus* breeding season to late in the *B. fowleri* season. The amount of overlap may well vary with local temperatures.

5. Isolation between the two forms based on difference in breeding season, response to calls or choice of breeding sites is ineffective. There also appear to be no intrinsic physiological barriers to inter-fertility.

6. The action of natural selection on these animals in their non-breeding habitats appears to be very rigid, and it is probably this which determines the characteristics of the populations.

7. Hybridization between the two forms has probably been greatly increased by deforestation of eastern hardwood forest areas.

8. The taxonomic position of the toads relative to each other has been discussed, and the possibility is suggested that they may be ecological subspecies.

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POLYMORPHISM AS AN OUTCOME OF DISRUPTIVE SELECTION

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The action of selection upon a character in a population of living organisms may be analyzed in terms of three elementary components: stabilizing selection, directional selection and disruptive selection (Mather, 1953). Stabilizing selection, by acting against the more extreme variants in the distribution of the character's expression, tends to narrow the variation, to make the population more uniform. The consequent responses in development may be various, and this component includes both the stabilizing and the normalizing selection which Waddington (1953) has distinguished by developmental criteria. The second type of action, directional selection, comes into play insofar as the mean expression of the character departs from the optimal: it tends to move the mean towards this optimum. The third and final component, disruptive selection, arises when several optima are favored.

The genetical consequences of stabilizing and directional selection have been discussed earlier (Mather, 1953), and some effects of disruptive selection have also been outlined (Darlington and Mather, 1949). Disruptive selection will, however, vary in its consequences according to the relations between the different optimal phenotypes and to the persistence and power of the selective forces favoring them. Not only the isolation, which Darlington and Mather discussed, but it would seem also polymorphism, can follow from disruptive selection.

Selection acts primarily on the phenotype, so that disruptive selection, if it is effective, must result in that adjusted discontinuity at the phenotypic level which is a feature of both isolation and polymorphism. In the case of isolation, however, this is accompanied by disruption of the erstwhile common gene pool, whereas in polymorphism the morphic types continue to share a common gene pool (apart from any switch genes that may be involved), on whose adjustment the polymorphism indeed depends for its efficient working. Thus polymorphism would seem to be a possible alternative to isolation as an outcome of disruptive selection, acting under conditions and in ways which we shall now examine; and being an alternative it is not necessarily a step on the way to isolation, even though both spring from the same type of selection.

Where variation in the environment results in different optima being favored in different groups of the population, the resulting tendency will be towards separate adjustment of the phenotype in the different groups and, ultimately, towards genetic isolation of these groups one from another (Mather, 1943; Darlington and Mather, 1949). Certain conditions must be fulfilled, however, if this tendency is to be effective. In the first place, the action of selection on the two groups must be separate in the sense that the optimal phenotype in one group must be uninfluenced by the optimal phenotype favored in the other: or, to put it another way, the optimal phenotypes must be independent of each other. This requires in effect that neither group is an effective part of the environment of the other.

Secondly, the groups must be sufficiently distinct from one another for the different forces of selection to be effective. This condition does not require that genetic exchange between the populations

is completely absent, but only that it does not rise above a certain maximum. Other things being equal the maximum will depend on the difference between the optimal phenotypes: the greater the difference, the higher the maximum exchange can be. It will depend also on the intensity of the selection. The higher the intensity, the higher the exchange can be; or, to put it the other way, the smaller the minimal effective difference between the optima can be for a given amount of exchange. Thus if selection intensifies, whether by increase in numbers or by any other increased stringency in the requirements for fitness, a difference in optima previously without effect can become effective in leading to isolation.

Exchange between the groups may be one of individuals by migration or of gametes by cross-breeding. In fact any agency which brings genes from one population into the other is an agency of exchange. The separation of the populations must therefore persist in time. This brings us to the third condition for the rise of isolation, that both the difference in environment from which springs the difference in optimal phenotype, and the separation of the populations, must be persistent. Given that these three conditions are satisfied (which must in general require spatial separation of the groups) genetic isolation, with its consequence of speciation, will be the outcome of disruptive selection.

Situations often arise in which not all of these conditions are fulfilled. The consequences of disruptive selection will then be of a different kind, as can perhaps be seen most obviously where the various optimal phenotypes are related to one another in a cross-breeding system which they jointly determine. The males and the females in a dioecious population, for example, will be subjected to different forces of selection and will represent different optimal phenotypes. These phenotypes are nevertheless tied together, for neither has any meaning except in relation to the other: each is an integral part of the other's effective environment. Thus there can be no tendency towards isolation because fertility and fitness depend on the cooperation of the two.

Since both male and female phenotypes must occur side by side in the same population, and since reproduction is by crossing, the general genotype which will be shared in a broad sense by all individuals, must be such as to give each zygote the possibility of developing either way, the capacity of approximating adequately to either optimal phenotype. At the same time, some agency must determine that one or other of these possibilities will be realized. Should either part of this dual system fail, the phenotype will depart unduly widely from both optima, and an individual suffering a selective disadvantage will result. We may pause to note that these are also the general requirements of any system of differentiation: indeed dioecy, heterostyly, incompatibility, or any cross-breeding system depending for its operation on diversity of phenotype may be regarded as a form of differentiation since they show the essential property of unlike entities arising to cooperate in the discharge of a single function, so that the entities themselves must be mutually adjusted for the efficient discharge of that function.

In the internal differentiation among the cells and tissues of a single individual, the course of development to be followed is determined immediately by the cytoplasm, though this, of course, will be reflecting in its constitution the earlier action of nuclear genes (Mather, 1948a and b). The differences between individuals upon which depend the cross-breeding system are sometimes determined in the same way, as for example in *Sciara,* where the sex differentiation depends on the cytoplasm received from the mother whose genotype its properties reflect; but other switching mechanisms also occur. In *Bonellia* determination is external: the presence of a female as a part of the immediate environment of a zygote determines the zygote's development as

a male. The most common switching mechanism for such breeding systems is, however, the segregation of a genetic difference. This difference may be simple or complex. It may range from what is apparently a single gene difference, as in the mosquito, to an aggregate of several chromosomes, as in bugs and hops. But so long as it segregates as a unit, it can act as a successful switch.

Physiologically the switch might be single in the sense that the organism has prospectively but two adjusted developmental paths so that whatever ramifications each may follow and however manifold the effect it may show, all the various consequences would follow from a single act of switching at a single period in development. The unity of the various features distinguishing the alternative phenotypes would then lie in the common system of canalization, in the developmental ties which the background genotype had imposed on them. Such is the nature towards which ancient polymorphisms, like the sex distinction in most animal groups, might be expected to tend.

In other, more recent, polymorphisms, however, the switch, though a unit in segregation, may be composite in action, behaving like a set of ganged switches which simultaneously turns over a group of electrical circuits. This we can see, for example, in the heterostyly system of *Primula* sp. where different parts of the switch super-gene control different and developmentally separable features or sub-characters of the heterostyly phenotype, one controlling stamen level, another stigma height and so on (Ernst, 1936; Mather, 1950). Rare recombination within the switch super-gene then gives new phenotypes having new associations of the sub-characters, but capable of successful functioning albeit as inbreeding instead of outbreeding individuals. Such, for example, are the homostyles which are found as a successful third type in some wild populations of the primrose (Crosby, 1949). The incompatibility switch gene in *Oenothera organensis* seems to be physiologically composite in the same way (Lewis, 1949), as does the X-Y difference in *Melandrium* (Westergaard, 1948). Sexual dimorphism in *Melandrium* and in animals such as *Drosophila* points the contrast between the newer and the more ancient polymorphisms; for breakdown in the plant results in potentially successful hermaphrodites, fertile as both males and females, and not in the sterile types characteristic of breakdown in the animals. Sexual dimorphism is not bound up with fertility in the newer system of the plant as it has come to be in the more ancient system of the animals.

In cases such as *Primula* and *Melandrium* the sub-characters are separately canalized, the sole coordination of their alternatives lying in the mechanical ganging of their various switches. The longer a polymorphism survives and the more ancient it becomes, the more likely the canalizations of its sub-characters are to become inter-woven with one another, so that any breakdown brought in by failure of the genetic system upon which depends the successful adjustment of development (whether through over wide crossing or undue inbreeding) will affect all of the sub-characters and not just a few of them differentially. At the same time the switch itself would seem likely to become a more integral part of the same system, depending like the canalization on numerical balance rather than on the presence or absence of a gene, supergene or chromosome segment.

These outbreeding systems afford convenient examples from which to discuss the conditions governing the origin and genetical structure of polymorphism, because the relations between their phenotypes are clear. On our present argument, however, we should expect polymorphism to arise wherever the various phenotypes favored by selection are bound together in function, no matter what the nature of the tie may be. Another clear case is afforded by Batesian mimicry in which the mimic, itself acceptable to the

predator, resembles a distasteful model, so securing by its mimicry a measure of protection from that predator (see Ford, 1953). In such mimicry the greater the relative number of mimics resembling a given model, the less successfully they can shelter behind its distastefulness, for the less likely the predator would be to come by experience to associate that appearance with distastefulness. Thus the more a species showing Batesian mimicry can spread its mimicry over a range of models, the greater the protection from predators its mimicry will offer to each individual. In other words, the success of each mimetic phenotype would be dependent on the frequency with which other individuals of the species displayed different phenotypes mimicing other distasteful models or showing no mimicry. A range of phenotypes would thus be advantageous, the advantage lying in the fact that each avoided queering the other's pitch. At the same time, each mimetic phenotype would have to be adjusted to resemble sufficiently closely its own model because intermediate phenotypes would enjoy the protection of neither model.

We have in fact the situation where a number of different optimal phenotypes would be advantageous, the phenotypes being tied together in that the success of each would depend on the frequency of the others, including non-mimetic phenotypes. For the inclusion of an adjusted proportion of a non-mimetic form in a population could lead, at least under certain circumstances, to a higher degree of individual protection than would be enjoyed if all individuals were mimetic, and indeed cases are not uncommon of populations which include non-mimetics alongside Batesian mimics. Each phenotype must thus be regarded as part of a system depending on the simultaneous occurrence of them all: each must be an effective part of the environment of the rest. Polymorphism should then be the result just as in the case of the system of outbreeding; and it should have a genetic basis similar in essentials to that of the polymorphic breeding systems, as indeed is found to be the case (Ford, *l.c.*). On the other hand, in Mullerian mimicry (as Ford points out) where distasteful species mimic one another for better mutual protection, diversity has not the same advantage and polymorphism would not be expected to arise—again as is observed to be the case. Indeed even a species in which Batesian mimicry is known would not be expected to be polymorphic outside the area where mimicry would serve as a protection (except insofar as the polymorphism is a relic maintained by secondary effects in the way to be discussed later): and again this appears to be substantiated by observation.

The tie between types, to which we are relating polymorphism, need not be at the level of external functioning, as it is in the cases of breeding systems and mimicry. Dobzhansky (1951) has shown that the sequentially different third chromosomes of *Drosophila pseudo-obscura* vary from one to another in the genes they carry, and that within a population sequential heterozygotes have an advantage over the corresponding homozygotes because they enjoy a higher genic heterozygosity which, within the genetic limits of the population, endows them with a greater individual fitness. Here the tie between the chromosome structures lies in their successful cooperation within the development of a single zygote rather than in the impact of different zygotes on one another. But the result is the same: polymorphism in respect of the sequential differences shown by the chromosome. The polymorphism shows itself, in fact, at the level of the tie, as we might expect.

Thus wherever we can discern a sufficiently strong tie, or cooperation, between structures or entities, whether of genetic structures within the nucleus, of cellular structures within the zygote, or of zygotes themselves within the population, we might expect to find all the features of polymorphism, viz., sharply delimited classes of the structure or entity

adjusted to work together for their common advantage, the adjustment depending on a common genotype which can ensure the necessary conditions, and on a switching systems whether environmental, segregational or cytoplasmic, to direct the structures into one path or the other. The switch may contain within itself part of the common genotype, as in Dobzhansky's chromosome polymorphism, or it may spring from the (in respect of the nucleus) outside effects of the common genotype as in differentiation, but in principle the distinction so clearly seen in zygotic polymorphism is always there.

The converse, that where there exists a polymorphism we might expect, if we search hard enough, to find a functional tie between the classes, is less readily demonstrable from observation and experiment: many cases of polymorphism are known where there is no obvious functional relation between the classes. The relation might, however, be of a subtlety which could elude any but the most direct search. One such possible relation could spring from changes or uncertainties in the selective forces themselves.

All species must be faced with a changing environment, but the reaction to these changes will not be uniform. The reactions will vary not only with the properties of the species themselves, but also with the nature and, from our point of view, with the period and distribution of the changes in circumstances. With persistent changes which affect a population generation after generation, and perhaps intensify as time goes on, direct genetical adjustment to the altered circumstances is the likely outcome, at least in species other than close inbreeders. If the change differs in its impact on different populations, the readaptation may well be accompanied by isolation and speciation. At the other extreme, changes which are short lived by comparison with the generation time, will evoke alterations in population size if they are spasmodic in occurrence. Where on the other hand they are sufficiently regular in recurrence as to be cyclical, and sufficiently widespread as to affect most if not all individuals, they will be accommodated by adaptation of the life history. Thus the alternation of day and night or of high and low tide can determine alternating states of activity and physiological function. Even the longer changes of season in the year can be met in the same way. The longer lived species may go into a seasonal rest either without change of form as in hibernation, or with it as in those plants where special organs like bulbs and corms are produced or where aerial parts are shed. In annual plants and animals too, where the period of life cycle has been brought to agree with the period of change, the more adverse season may be faced in some resting form such as seed or resistant egg. But where changes occur and recur so that they are not truly persistent and yet have a period longer than the generation time, and perhaps even more particularly, where they are spasmodic in distribution within limits to be discussed later, the response of the species must be different.

Perhaps the clearest example of cyclical changes of period longer than the generation is to be found in the seasonal changes with which ephemeral plants and animals are faced. Each generation is faced with a different environment, but the changes come full circle every few generations. Where the individuals of a generation are the immediate progeny of the generation before, the success of the species depends on sufficiently good adjustment of individuals to circumstances which were foreign to their immediate ancestors. Direct selective responses would thus offer no advantage and might well be actively disadvantageous. Various other possibilities exist for phenotypic adjustment. Sometimes an intermediate phenotype, adjusted to the average needs of the different generations could suffice, or a continuously varying plasticity of development in response to external circumstances could meet the

changing conditions; but where the generations met sharper differences in environment or where intermediate phenotypic properties were unsatisfactory, a polymorphism in time could follow. The genotype would be adjusted to offer alternative lines of development, which would be switched by external conditions. Such polymorphism in time is known for example in the seasonal parthenogenesis of aphids and in the seasonal change of sex chromosome behavior in the moth *Talaeporia* (see Darlington and Mather, 1949). Dr. Ford has also drawn my attention to the examples of the wet and dry season forms of the butterfly *Precis sesamus* and the spring and summer forms of *Araschnia levana*. The tie between phenotypes in such cases lies in the dependence of each on the other for continued propagation under conditions which would be adverse to itself.

To regard such cyclical changes as a form of polymorphism is to extend this concept in a material way, since the alternative forms are not characteristically present in the population simultaneously. As in polymorphic populations, however, the forms of a cyclically changing group are integral parts of one another's ancestry so that they must share a common genetical adjustment. Thus, the genetical structure of cyclically changing populations will involve a common background capable of giving two (or more) distinct but adjusted paths into one or other of which development will be switched, just as is the case in polymorphic populations (albeit that the switch is environmental rather than genic). In this respect cyclical changes and polymorphism stand in contrast to cases of geographical variation where the races live in different places, form no regular part of one another's ancestry, and hence will achieve adjustment by separate and not necessarily related genetic changes instead of by the emergence of a common genotype characterized by its capacity to offer alternative channels of development. Some types of spatial separation might, however, also lead to a genetical structure which we should recognize as polymorphism, as we shall see later.

Successive polymorphism of the kind shown by the aphids and other insects can (and, if there is any overlap of the generations, in general will) lead to simultaneous polymorphism with the forms present side by side at least at some season. It could therefore be regarded as an extreme form of cylical change in frequencies of the morphic types in the population. Less extreme cyclical changes in frequency are known, for example in respect of color pattern in the ladybird *Adalia bipunctata* (Timofeeff-Ressovsky, 1940) and in respect of third chromosome sequences in *Drosophila pseudoobscura* (Dobzhansky, 1947), where no type ever vanishes from the population at one season to reappear at another. But these differ from the true cases of successive polymorphism in that they may depend on switching by a simple genic segregation, which cannot be the case where types successively vanish and reappear in the population and where switching will be most simply achieved environmentally. Indeed the seasonal changes of frequency in *Drosophila* are almost certainly, and in *Adalia* very likely, secondary effects of a polymorphism which exists for other reasons. These reasons we have already discussed in the case of *Drosophila*.

A kind of simultaneous polymorphism depending for its maintenance on successive change is perhaps that of clutch size (2 or 3 eggs) in the swift (see Lack, 1954). The genetical system underlying this behavior may well, however, differ from that which we can see at work in the cases considered above. Clutch size is obviously a meristic character so that variation in the phenotype must be discontinuous, even though there be continuous variation in the underlying genetic potential of egg production. Thus it may be that the general genotypes of the 2 egg and 3 egg swifts differ genetically, the discontinuity being imposed by the nature of the phenotypic variation, rather

than that they represent the end products of alternative developmental paths generated by the same general genotype and switched by a specific mechanism. The verification of this interpretation would require genetical experiments and observations which might be impossible with these birds; but if it be true it would serve to emphasize once again how similarities at the phenotypic level can spring from a variety of genetic systems. Having different properties these systems will arise in different ways and will be subject to different kinds of change should the selective situation alter.

Environmental conditions must always vary in space as well as in time. Such variations as occur within the range of regular movement or experience of a single individual will be expected, like short-period changes in time, to be accommodated by the appropriate behavior of that individual; for example, by the avoidance of a distasteful area by an animal or growth away from a dark corner by a green plant. Differences between environments so widely separated that once individuals or descendants have passed from one to the other there is but little chance of a return, are likely to bring about new permanent genetic adjustments just as do long term changes in time. But, again as with changes in time, there is a degree of separation in space too large for an individual to be regularly encountering the two environments, but small enough for the offspring of an individual in one environment to be likely, but not certain, to find itself in the other. Again, a developmental plasticity of phenotype could offer the ability of adjustment to whichever environment is in fact encountered, or if the selective requirements of the environments are not too severe, some intermediate phenotype might fit both sufficiently well. If, however, high adjustment is required in each environment, as is possibly the case where for example properties of camouflage are concerned, polymorphism might well be favored, so that an individual of one morphic type adjusted to one environment would produce offspring of both kinds. Not matter which environment was then encountered some of the offspring would fit it.

The tie between the types is once again the dependence of each on the other for the maintenance of the lineage in generations that happened to encounter the alternative circumstances. Such polymorphism would be favored only where the loss through elimination of the unadjusted type was less than the loss which would follow from the partial maladjustment in both environments which a common continuously varying range of intermediate phenotypes would involve. The ability to choose an environment which mobility confers on an organism might well reduce the loss in the case of polymorphism and so increase the chance of its occurrence.

The relations between the types which constitute a polymorphic series may be complex. The polymorphism is commonly described and discussed in terms of a single obvious difference of form or color; but as Hovanitz (1953) has in fact shown for the butterfly *Colias*, other differences in, for example, behavior may be associated with the color. The cuckoo perhaps represents a further example of complex polymorphism, the gentes differing in a number of correlated characters (see Southern, 1954). The genetical relations of the gentes are far from clear, but the at least surface resemblance of cuckoo mimicry to Batesian mimicry requires no emphasis. In the *Colias* butterflies the differences in color and behavior have been observed to be jointly switched by a single unit of genetical segregation, but as we have already seen, such a unit is not necessarily also a unit of gene action. Indeed it would seem more likely that in at least the majority of cases the unit of segregation would be a super-gene containing a number of units of action similar to the genetic switches

we have already seen to be involved in, for example, the control of heterostyly in *Primula*. The tight linkage characteristic of a super-gene could itself be the outcome of selection (Fisher, 1930; Mather, 1943; Sheppard, 1953b).

Once a system of polymorphism has arisen it will not be expected to remain static, but to show certain secondary developments. Ford (1953) has pointed out that not only would genotypes distinguished by rare combinations of the switching alleles be expected because of their rarity to tend towards reduced viability, extending even to lethality, but that this is in fact observed in wild polymorphic species. It has also been shown by Darlington (1939) that a genetical switching difference once established will tend to grow. Darlington's discussion centered on sex inequalities, but his conclusions are of wider validity. Once polymorphism was established in respect of any one character, further characters could be brought into the morphic differences by growth of the switching differences towards a super-gene, without the rise of an entirely fresh switching system. The later development could thus be built onto the earlier structure. In this way an existing polymorphism might well act as a focus for the growth of new differences. Furthermore it would seem by no means impossible, nor even unlikely, that as time went on characters which were secondary in origin became primary in effect, so that the original difference in respect of which the polymorphic system was first built up lost its importance and persisted only by virtue of its association with characters added later to the system. In such a case the original and perhaps most obvious difference between the morphic types could offer little or no information about the relations upon which depended the advantage, and hence persistence, of the polymorphism.

In addition to this tendency for the morphic differences to change and grow there is a further agency which must make for instability in a polymorphic system. Although, where the view we have been discussing is correct, there must be a tie between the types in respect of some function or functions, in respect of other functions individuals of different types must compete like any others. The cooperation must outmatch the competition if the less favored morphic type is to be held in the population, but the competitive balance will itself determine, at least in large measure, the relative frequencies of the types. Thus, over a range of environments, we may see variation in the frequencies of the types. Such are the clinal changes in the frequencies of yellow and white butterflies which Hovanitz reports in the species of *Colias*. Furthermore, under extreme conditions the tie between unlike types may be insufficient to outweigh the competition with the result that one type is lost, again as Hovanitz has observed. Either a lessening of the importance of the cooperative function or an increase in the stringency of competition could lead to an alteration in the relative frequencies of the types within an existing polymorphic population (as has been observed by Sheppard (1953a) in the moth *Panaxia*), or even to the polymorphism itself vanishing.

A further possible change remains to be noted. Polymorphism may encourage outbreeding, either as its primary effect as with dioecy or incompatibility, or as a secondary consequence as in *Panaxia* (Sheppard 1952); but whether itself affecting the breeding structure or not, polymorphism must in all cases arise in populations of outbreeding individuals, for the reason that even though the ties between the types need not depend on cross-breeding or segregation, the adjustment of the genotype necessary to delimit the appropriate channels of development would be debarred by the genetical rigidity of complete inbreeders. But, for reasons which may or may not be connected with the polymorphism, inbreed-

ing may supervene on cross-breeding (Mather, 1943; Darlington and Mather, 1949). Should this take the form of a disproportionate restriction of mating between the morphic types, these would be partially isolated and their isolation would then tend to strengthen towards the final outcome of speciation into groups delimited by the characteristics of these types. The obvious phenotypic differences between the new species would thus be those associated with the old switch gene or super-gene (for only genetically switched differences would be retained in such a break-up), and so would appear to be inherited simply, though the essential differences between the species—the differences producing isolation—would be genetically complex. These new differences would be superimposed on the polymorphism, and would not spring essentially from it. Thus the genetical differences originally associated with the old polymorphism need give no clue to the true genetic differences between the new species.

It should be observed that the new species need not occupy the same territory. Insofar, for example, as the move towards restricted mating arose from a need for increased local adaptation, geographical considerations must enter in. Then with the new balance of competition and cooperation, one of the old morphic types might be fixed as the new species in one area and a different one in another, while the polymorphism might be retained where cooperative advantage still outweighed competition in the new locally adjusted specific group of a third place.

Dr. P. M. Sheppard has drawn my attention to relationships in the swallowtail butterflies which may well be examples of such a situation. *P. zelicaon* is polymorphic for larval spot color, which depends on one or possibly two genes. In other North American species polymorphism is rare or absent, and the European *P. machaon* is monomorphic. Also, *P. machaon* and *P. zelicaon* are uniform for yellow ground color in the wings while *P. asterius* and *P. brevicauda* are uniform for black, which differs from yellow in one gene. A fifth species, *P. bairdii* in North America, appears to be polymorphic for this character, though there is still a little doubt whether this is a true polymorphism or whether it springs from hybridization in a zone of contact between yellow and black forms. It does seem, however, that differences which appear as polymorphism in one species may distinguish other species, each of which is uniform for its feature. The genetical study of these swallowtails, begun by Clarke and Sheppard (1954), will clearly be of great interest in seeking to understand the relations between polymorphism and species differences.

Should the inbreeding which supervened in a polymorphic population be more general in its incidence, reducing cross-breeding between individuals of the same as well as of different types (as would be the case with self-fertilizing mechanisms in plants) no special isolating mechanism would arise, for the inbreeding mechanism would, when sufficiently well developed, secure isolation. We should then have a situation where the individuals could be classified into "species" phenotypically distinguished by the characters of the types which formed the parts of the old polymorphism, though capable, following accident or experimental intervention, of breeding as freely between the "species" as within them. Such is the situation within the groups of wheat or oats where the "species" have a common chromosome number. The "species" in these and similar groups, often cited as examples of the importance of major genic differences in speciation, could in fact be nothing more than the relic of an ancient polymorphism which lost its essential unity when inbreeding overlaid outbreeding as so clearly happened in these cereals. And the major genes, or more precisely supergenes, distinguishing the "species" could be nothing

more than the relic of the ancient switching system, first evolved and developed for controlling differences within populations, but, having run its full course by losing its switching function, now remaining as an accidental marker between some of the individuals cut off from one another by the general inbreeding mechanism.

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STUDIES OF LINKAGE IN POPULATIONS. I. ASSOCIATIONS OF SECOND CHROMOSOME INVERSIONS IN *DROSOPHILA ROBUSTA*

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INTRODUCTION

Despite recent progress in the development of population genetics in relation to evolution, studies of actual populations continue to lag far behind the theoretical work. This is particularly evident in problems concerning linkage. Mathematical studies of the disposition of linked loci under randon mating appeared early in the history of modern genetics (Weinberg, 1909, and Robbins, 1918), but few data bearing on their predictions have appeared in the literature. The present paper reports a study of linked gene arrangements in natural populations of *Drosophila robusta* Sturtevant. Certain of the arrangements are found to be present in non-random combinations. The deviations from independence apparently depend on selection which differentiates not only between different combinations of the arrangements but also between similar combinations in which the components occupy different positions in the cell. If this interpretation of the data is correct, these are the first position effects to be noted in natural populations and the data point to a new method for discovering the phenomenon.

TERMINOLOGY AND NOTATION

Chromosomal aberrations have been studied for over thirty years. Nonetheless, no standard term has come into practice to designate in a general way the aberrations carried by an individual to correspond to the term "genotype" used in relation to the genes. In fact, many authors refer to inversion homozygotes or heterozygotes as "genotypes" when, in the usual sense of the term, it could easily happen that two individuals carrying the same inversions have different genotypes even for the loci embraced by the inversions. This may lead to confusion. Carson (1953) has substituted a better term, "structural karyotype," and a shortened form of this, "karyotype," will be used in the present paper. The excellent short-hand notation Carson (1953) introduced for the inversions of *D. robusta* will also be followed here, particularly in the tables. The additional term "linkage type" will be used here to distinguish flies which have the same inversions (hence, the same karyotype) but in different spatial arrangements or linkages. For example, individuals having 2L-3 and 2R on one second chromosome and 2L and 2R-1 on the homologous chromosome (written 3S/S1 in the shorthand notation) have the same karyotype (S/3, S/1), but are a different "linkage type," from individuals having 2L and 2R on one chromosome and 2L-3 and 2R-1 on the homolog (linkage type SS/31). The gene arrangements referred to, along with the others to be mentioned in this paper, are described by Carson and Stalker (1947).

MATERIALS AND METHODS

Adult *Drosophila robusta* were collected during 1950, 1951, and 1952 (and some in 1953) in Crumpacker Woods near Blacksburg, Virginia and during 1952 and 1953 in Heth's Woods, located about two miles from Crumpacker. Crumpacker Woods was described in a previous publication (Levitan, 1951b). Heth's Woods contains much the same type of vegetation, but has been somewhat less disturbed by activities of man. The methods of collection in both woods were very similar to those described by Levitan (1951a). The reader is also referred to the above-mentioned papers (Levitan, 1951a and 1951b) for the methods used to analyze the 1950 collections for gene arrangement frequencies. The data suggested selectional differences between males and females carrying the same ar-

rangements (Levitan, 1951b), but the results were weakened by the small amount of information available concerning the Spring females, since these females were usually inseminated when collected. To correct this situation, two additional procedures were adopted for the analysis of collections made after 1950: (1) if readily available, the salivary glands from several, rather than single, larvae from each inseminated female were smeared and recorded (though, as before, only the first female larva contributed to the "egg sample" portion of the frequency count of the arrangements). (2) The females were despermed, by repeated individual transfers, in culture vials, until successive vials which each had inhabited for at least ten days showed no larvae. The females were then analyzed in the same manner as the virgin females. While greatly increasing the labor involved, these added procedures, particularly the desperming, have greatly strengthened some of the crucial data of the present paper.

Accuracy of the Data

The data discussed here consists mainly of the 293 adults from these populations who proved to be of karyotype 2R/2R-1 with variable karyotype for the left arm of the same chromosome. Since these individuals constitute only 13.6% of the 2,161 adults analyzed, the following question may be raised: what proportion of the other 86.4% have been classified as homozygotes for the right arm as a result of chance errors but properly belong among the data presented here (with the possibility of upsetting the conclusions drawn). This question will be discussed separately for the two sexes.

Males. The analysis of the males has the highest degree of accuracy. Of the 85.9% analyzed as homozygous for right-arm arrangement (S/S or 1/1), approximately three-fourths are known to be heterozygous for left-arm arrangements. These cannot have been misclassified for the right arm, for no crossing-over occurs in *Drosophila* males. The problem then concerns only the 20% or so which appear to be homozygous for both right- and left-arm arrangements. Their analysis usually depended on the examination of eight larvae from each cross to homozygous laboratory females of known constitution. In the rare instances when eight larvae were not available, the indicated karyotype was not recorded unless data was present from at least six larvae. Counterbalancing these were several instances when *more* than eight larvae were observed (either when an analysis was accidentally repeated or when more larvae were smeared to check on a doubtful result in another chromosome). The probability of chance error is therefore about one chance in 128 in the analysis of the 20% of males judged doubly homozygous in this chromosome, or less than 2 chances per 10,000 male analyses, a negligible quantity for which to correct in the total of 1209 males actually studied.

Females. As in the males, the conclusion that a female was homozygous for arrangement usually depended on the finding of eight larvae in succession which received that arrangement from her. Hence, as a first approximation, the probability is that about 1/128 of those classified 2R/2R or 2R-1/2R-1, or about 0.7% of the 952 female analyses, were erroneous due to chance misclassification of heterozygotes. The true probability of these errors is less than this, for the following reasons:

a. 186 of the females were also studied for recombination of X-chromosome inversions (Levitan, 1953 and unpublished data). For most of these the glands from more than eight larvae were examined.

b. In addition to the eight larvae obtained from crossing a despermed female to stock males, a number of larvae from her mating in nature were commonly recorded (as already described). In many instances all of these larvae were in agreement in indicating the mother was 2R/2R. Hence, the probability that she was indeed homozygous was often greater than 127/128. (An exact evaluation of the probability is difficult because of a bias factor, the fact that the analysis of a rarer, 2R-1/2R-1, female could not be aided by this type of data.)

c. Carson (1953) and the writer (Levitan, 1953 and unpublished data) have found that in females heterozygous for inversions on both arms of the second chromosome recombination between these inversions occurs only rarely when the female is not simultaneously heterozygous for inversions on both arms of the X and on the right arm of the third chromosome. Slightly less than 10% of females in the populations studied presented these conditions in X and 3 which favor recombination in 2. Those of the remaining 90% that are known to be heterozygous for arrangements in the left arm of the second chromosome (about 75% of them) are therefore determined with almost the same certainty as the corresponding males.

TABLE 1. *Actual (a) and expected (e) numbers of second chromosome karyotypes in adult* D. robusta *collected near Blacksburg, Virginia, 1950–53*

	Crumpacker Woods				Heth's Woods				Both woods Both sexes	
	Females		Males		Females		Males			
	a	*e*	*a*	*e*	*a*	*e*	*a*	*e*	*a*	*e*
S/S, S/S	39	34.87	34	43.67	28	24.08	27	25.41	128	128.03
1/1, S/S	24	21.33	19	25.19	14	19.21	32	24.98	89	90.71
2/2, S/S	20	15.65	18	20.25	1	4.70	7	7.24	46	47.84
3/3, S/S	68	58.95	85	76.27	44	46.74	64	55.25	261	237.21
S/1, S/S	56	54.54	58	66.34	42	43.02	48	50.39	204	214.29
S/2, S/S	45	46.72	64	59.48	17	21.27	30	27.13	156	154.60
S/3, S/S	79	90.67	128	115.43	63	67.10	73	74.94	343	348.14
1/2, S/S	24	36.54	57	45.18	20	19.00	24	26.90	125	127.62
1/3, S/S	78	70.92	87	87.67	66	59.93	63	74.31	294	292.83
2/3, S/S	58	60.75	72	78.61	39	29.64	39	40.01	208	209.01
S/S, S/1	8	5.21	10	8.16	3	3.43	2	3.82	23	20.62
1/1, S/1	3	3.19	7	4.71	5	2.73	2	3.76	17	14.39
2/2, S/1	7	2.34	1	3.79	0	.67	2	1.09	10	7.89
3/3, S/1	6	8.80	8	14.26	2	6.65	4	8.31	20	38.02
S/1, S/1	5	8.14	15	12.40	6	6.12	4	7.58	30	34.24
S/2, S/1	6	6.98	13	11.12	4	3.02	5	4.08	28	25.20
S/3, S/1	16	13.54	20	21.58	12	9.54	16	11.26	64	55.92
1/2, S/1	9	5.46	9	8.44	3	2.70	8	4.04	29	20.64
1/3, S/1	7	10.60	18	16.38	8	8.52	18	11.18	51	46.68
2/3, S/1	6	9.08	8	14.70	6	4.22	1	6.02	21	34.02
S/S, 1/1	1	.19	1	.38	0	.12	0	.14	2	.83
1/1, 1/1	1	.12	1	.22	0	.10	0	.14	2	.58
2/2, 1/1	0	.09	2	.18	0	.02	0	.04	2	.33
3/3, 1/1	0	.33	0	.67	0	.24	0	.31	0	1.55
S/1, 1/1	0	.30	2	.58	0	.22	0	.28	2	1.38
S/2, 1/1	0	.26	1	.52	0	.11	0	.15	1	1.04
S/3, 1/1	0	.51	0	1.01	0	.34	1	.42	1	2.28
1/2, 1/1	0	.20	0	.39	0	.10	0	.15	0	.84
1/3, 1/1	0	.40	0	.77	1	.30	0	.42	1	1.89
2/3, 1/1	1	.34	1	.69	0	.15	0	.23	2	1.41
Total	567	567.02	739	739.04	384	383.99	470	469.98	2,160	2,160.03

TABLE 2. *Frequencies, in per cent, of second chromosome gene arrangements in adult* D. robusta *collected near Blacksburg, Va., 1950–53*

Woods	Sex	*n*	2L	2L-1	2L-2	2L-3	2R	2R-1
Crumpacker	Females	1,137*	26.65	20.84	17.85	34.65	93.05	6.95
	Males	1,486†	26.58	20.19	18.10	35.13	91.45	8.55
Heth	Females	768	26.82	23.96	11.85	37.37	93.36	6.64
	Males	944‡	25.00	24.79	13.35	36.86	93.01	6.99

* Includes one *2L-1 2R* chromosome from an incomplete analysis; and one *2L-3 2R* from 3S/5S female (see text) in addition to material in table 1.

† Includes 3 *2L 2R*, one *2L 2R-1*, one *2L-2 2R*, one *2L-2 2R-1*, and two *2L-3 2R* chromosomes from eight incomplete analyses.

‡ Includes one *2L 2R*, one *2L-1 2R-1*, one *2L-2 2R*, and one *2L-3 2R-1* from four incomplete analyses.

RESULTS

In table 1, 2,160 adults completely analyzed for second chromosome arrangements are classified according to the thirty structural karyotypes of this chromosome (in columns headed "a"). (One Crumpaker female, structurally 3/5, S/S, is omiteed from table 1, and her chromosome *5S* is omitted from later tables, because arrangement 2L-5 (Levitan, 1951c) was not found again in these populations.) The table 1 columns headed "e" give the numbers of each karyotype that would be expected on the assumptions (1) that the Hardy-Weinberg formula is applicable and (2) that the arrangements of the left-arm are independent of those on the right-arm. These expected numbers were calculated on the basis of the arrangement frequencies in each adult sample (table 2). Because of heterogeneity in the frequencies shown in table 2, expected values for "total" samples (e.g., "Both Woods, Both Sexes") were *not* calculated from their arrangement frequencies; they are, in-

TABLE 3. *Chi-squares, testing goodness of fit, described in this paper*

Row	Data tested	d.f. in each sample	Crumpacker Woods			Heth Woods			Both woods		
			Females	Males	Both sexes	Females	Males	Both sexes	Females	Males	Both sexes
1	All Karyotypes (table 1)	16	28.2*	23.0	17.2	17.8	27.5*	20.9	22.9	25.8	23.2
2	Left arm Karyotypes (table 1)	6	10.4	7.9	3.7	10.2	3.6	2.3	6.0	8.6	2.1
3	Right arm Karyotypes (table 1)	1	0.03	1.6	1.3	0.3	0.7	1.0	0.1	0.4	0.1
4	Row 1 minus rows 2 and 3	9	17.8*	15.5	12.2	7.3	23.2†	17.6*	16.8	16.8	21.0*
5	Karyotypes, tables 1 and 3	22	30.8	41.3†	35.0*	33.7¶	42.0†	37.1*	27.1	56.4§	46.4†
6	Row 5 minus rows 2 and 3	15	20.4	31.8†	30.0*	23.2¶	37.7‡	33.8†	21.0	47.4§	44.2‡
7	Chromosomes (table 5)	4	3.6	25.2§	25.6§	6.7	15.1†	7.6¶	1.3	40.3§	28.2§
8	Chromosomes, not incl. 2L-3	3	1.9	10.5*	11.1*¶	6.1	6.9	4.8¶	1.1	17.5‡	12.6†¶
9	Carriers of 2L-3 and 2R-1 (table 6)	1	1.4	3.6	4.9*	0.03	0.1	0.01	0.8	1.7	2.8
10	Carriers of 2L-3 linked to 2R-1 (table 6)	1	3.1	14.9‡	17.0§	0.05	4.3*	2.8	2.3	18.8§	18.4§
11	3S/31 (table 1)	1	0.9	2.8	3.6	3.3	2.3	5.5*	3.7	5.0*	8.7†

* P less than 5%.
† P less than 1%.
‡ P less than 0.1%.
§ P less than 0.01%.
¶ P would be lowered to a significant level (or, if significant, lowered to a higher order of significance) if doubtful females (see text) were reversed.

stead, sums of expected numbers in the component samples. (For example, a total sample for males of both woods could be constructed from the data of table 1. Its expected number for karyotype S/S, S/S would be 43.67 plus 25.41, or 69.08, etc.) The samples shown (e.g., Crumpacker males) also consist of combined material, including significant heterogeneities. So detailed a presentation of the data as would be necessary to eliminate these pooling errors would, however, excessively lengthen this paper. Preliminary calculations for a paper describing seasonal aspects of the data indicate the errors are quite small. They rarely exceed 2% of the expected value obtained here, and in no instance are they greater than 1.00.

Chi-squares testing the goodness-of-fit of the data in table 1 (and of "total" samples derived from them) to the corresponding expected values are shown in row 1 of table 3. The 2R-1/2R-1 were treated as one class in all calculations, expected values of individual karyotypes being consistently less than 1.00. Two of the nine sample chi-squares have P below 5%. Their significance may, however, be spurious, inasmuch as both samples contain expected values below 5. Such expected values make the P value in the table of chi-square smaller than the true P (Cochran 1942).

If the samples are tested only for goodness-of-fit of the karyotype of each arm to the Hardy-Weinberg Law, none of the samples are significant (rows 2 and 3, table 3). Subtracting these chi-squares from the ones in Row 1 gives chi-squares (row 4) which are a measure of the variability of the table 1 data with respect to independence between the arms. Four of the samples are now significant, though for one (Crumpacker females) this may again be spurious. This suggests that the populations, while in random mating equilibrium for each arm, contain evidence of non-independence between arms.

This suggestion is greatly strengthened when the karyotypes which are heterozygous for arrangements in both arms are divided into their component linkage-types (table 4). The exact linkage relationship could not be determined in six females (one S/1, S/1, one S/2, S/1, and one 1/2, S/1 from the Crumpacker Woods; two S/3, S/1 and one 1/3, S/1 from Heth's Woods) because recombination between the inversions was not significantly different from 50%. They are listed as S1/1S, SS/21, 1S/21, SS/31 (two), and 1S/31, respectively. The effect of reversing this disposition will be noted. Each linkage type has an expected value which is half of the corresponding table 1 karyotype's "e." If the twelve linkage types of each sample are now substituted for the six doubly-heterozygous karyotypes in a test of goodness-of-fit of the data in table 1 to expected values, the chi-squares shown in row 5 of table 3 are obtained. Six of the nine are significant, four at the one per cent level; one more sample would be significant if disposition of the doubtful females were reversed. Again several of the significant samples contain classes with expected values less than 5, so that the indicated P values are too low. If the deviation for each class with expected value less than 5 were diminished by 0.5, however, these samples remain significant at the 5% level. This is a rather severe test, inasmuch as the procedure (Yate's correction) was designed for contigency tables with one degree of freedom, and the effect of expected values below 5 diminishes as the number of degrees of freedom increase (Cochran, 1942, 1952). Hence, the conclusion that many of these samples probably do not fit the expected values is strongly reinforced. That this is related to the relationship between the arrangements of the two arms is further indicated by the even lower P's when the chi-squares testing fit to the Hardy Law are removed (row 6, table 3).

The data of table 4 provide evidence of non-random relationship between left- and right-arm arrangements in another way, one whose validity is not affected by pool-

TABLE 4. *Linkage types of* D. robusta *adults heterozygous for inversions in both arms of the second chromosome*

Linkage type	Crumpacker Woods			Heth's Woods			Both woods		
	Females	Males	Total	Females	Males	Total	Females	Males	Total
SS/11	2	9	11	4	2	6	6	11	17
S1/1S	3	6	9	2	2	4	5	8	13
SS/21	2	4	6	2	1	3	4	5	9§
S1/2S	4	9	13	2	4	6	6	13	19
SS/31	6	3†	9†	10*¶	5	15	16	8‡	24*
S1/3S	10	17	27	2	11	13	12	28	40
1S/21	4	3	7	3	4	7	7	7	14
11/2S	5	6	11	0	4	4	5	10	15
1S/31	3	5	8	1§	4*	5†§	4§	9†	13‡
11/3S	4	13	17	7	14	21	11	27	38
2S/31	2	2	4	4	0	4	6	2	8
21/3S	4	6	10	2	1	3	6	7	13
Totals	49	83	132	39	52	91	88	135	223

* Deviation from 1:1 ratio significant at 5% level.
† Deviation from 1:1 ratio significant at 1% level.
‡ Deviation from 1:1 ratio significant at 0.1% level.
§ Deviation from 1:1 would have higher degree of significance, i.e., P would be lower, if doubtful females (see text) were counted in the opposite type.
¶ Deviation from 1:1 would not be significant if doubtful females (see text) were counted in the opposite type.

ing errors in the expected values. As was noted above, the two linkage types corresponding to a given karyotype are expected to be present in equal numbers. The probability that the two linkage types of the same karyotoype deviate significantly from a 1:1 ratio, using both tails of the binomial, was calculated (with the help of the convenient table of Cole, 1945, for the smaller numbers), and, if so, this fact entered in table 4. Nine of the 54 groups of linkages show significant deviations from equality, six of them at the 1% level. Three others would be significant if certain doubtful females were reversed, though reversing could also remove one group from the significance point. As in the material of lines 5 and 6 of table 3, the "total" samples, for both woods together or for both sexes together, commonly show higher degrees of significance than that of their component samples. This indicates that results which are not significant often show the same tendencies as the significant results, so that their sum, constituting a larger sample, has lower probability that the deviation is due to chance or sampling error. The opposite phenomenon characterizes the material with generally non-significant results (lines 1–3 of table 3); here the deviations of summed samples are commonly of opposite sign and cancel one another out, as is expected when chance alone is responsible for the deviations.

Inspection of the data, particularly of the significant samples, discloses that the deviations show further consistencies. For one thing, there is more tendency for data concerning males to be significant, particularly at Crumpacker Woods and in the combined sample, than data of females. Also, the linkage types containing chromosomes *S1*, *11*, or *3S* commonly exceed their expected values, whereas those

containing their opposite numbers, *SS*, *1S*, or *31*, are usually deficient. These regularities are made more evident by constructing a table which shows the number of the eight kinds of chromosomes present (table 5). Since all the chromosomes are from individuals who are S/1 in the right arm, it follows, as for the material in table 4, that the two linkage forms containing the same left-arm arrangement should be equal if the left- and right-arm arrangements were independent. The chromosomes with the same left-arm arrangement in the samples are grouped together in table 5. In many cases the numbers in the same square show large deviations from equality. Chi-squares testing these deviations were calculated, and the fourteen squares with significant deviations are appropriately marked in the table. Also, the sums of the 4 chi-squares pertinent to a sample are entered in table 3 (row 7).

The consistencies noted about the linkage types are seen again. The excess of *3S* over *31* is particularly clear. Row 8 of table 3 shows, however, that the sums of the chi-squares for males and for "both sexes" in Crumpacker and in the combined sample are significant even when the *3S* vs. *31* data are not considered, because, primarily, the males of both woods have a much larger number of *S1* and *11* than *SS* and *1S*, respectively. The greater tendency for male than for female data to show significant deviations is also underscored by the fact that all of the chi-squares for male data in row 7, and two of the three in row 8, of table 3 are significant, but none of the corresponding female chi-squares are significant. Similarly, nine of the twelve pairs of male data (table 5) have deviations from 1 : 1 with P less than 10%, only one of the twelve female pairs having that great a deviation. Although the females tend to show no significant deviations, the ratios of linkage forms in their Crumpacker samples concerning 2L and 2L–3 and in their Heth samples concerning 2L–1 are in the same direction as in the male data.

The conclusion is inescapable that, at least in males who are heterozygous for inversions in both arms of the second

TABLE 5. *Second chromosomes in adult* D. robusta *of table 4*

Chromosome	Crumpacker Woods			Heth's Woods			Both woods		
	Females'	Males	Total	Females	Males	Total	Females	Males	Total
SS	10	16	26	16	8	24	26	24	50
S1	17	32*	49†	6*¶	17	23	23	49†	72*
1S	10	14	24	6	10	16	16	24	40
11	11	28*	39‖	11	20	31*	22	48†	70†
2S	11	17	28	6	8	14	17	25	42
21	10	13	23	7	6	13	17	19	36
3S	18	36	54	11	26	37	29	62	91
31	11	10‡	21‡	15	9‡	24‖	26	19§	45§
Total	98	166	264	78	104	182	176	270	446

* Deviation from 1:1 significant at 5% level.
† Deviation from 1:1 significant at 1% level.
‡ Deviation from 1:1 significant at 0.1% level.
§ Deviation from 1:1 significant at 0.01% level.
‖ Deviation from 1:1 would be significant at 5% level if doubtful females (see text) were reversed.
¶ Deviation from 1:1 would not be significant if doubtful females (see text) were reversed.

TABLE 6. *Analysis of table 1 and table 3 karyotypes containing 2L-3 and 2R-1*

Sample	Karyotypes with 2L-3 and 2R-1, not necessarily linked		Karyotypes with 2L-3 linked to 2R-1		All karyotypes*	
	a	*e*	*a*	*e*	*a*	*e*
Crumpacker females	36	43.60	18	26.99	567	567.02
Crumpacker males	55	70.06	19	43.73	739	739.04
Crumpacker, both sexes	91	113.66	37	70.72	1,306	1,306.06
Heth females	29	29.96	18	18.82	384	383.99
Heth males	40	38.15	14	23.92	470	469.98
Heth, both sexes	69	68.11	32	42.74	854	853.97
Both woods, females	65	73.56	36	45.81	951	951.01
Both woods, males	95	108.21	33	67.65	1,209	1,209.02
Both woods, both sexes	160	181.77	69	113.46	2,160	2,160.03

* Necessary for calculation of "other karyotypes" cells of the chi-squares shown in rows 9 and 10, table 3.

chromosome, arrangements 2L, 2L–1, and 2L–3 are not independent of 2R and 2R–1. 2L and 2L–1 are linked with 2R–1 more than with 2R. 2L–3, on the other hand, is mostly linked with 2R. One arrangement, 2L–2, fits the hypothesis of independence from 2R and 2R–1 in all the data.

DISCUSSION

Three hypotheses to account for the lack of independence between left-arm and right-arm arrangement may be considered: First, that it is a relic of the mode of origin of the arrangements. Second, that it is the result of selection for phenotypes produced by interaction of genes in a left-arm arrangement and genes in a right-arm arrangement. Third, that it is the result of selection for phenotypes dependent on having genes of the two arms in specific positional relationship, i.e., on position effects. A careful consideration leads to the conclusion that only the position effect idea can explain the data.

Under the first hypothesis the differences between *2L–3 2R* and *2L–3 2–R1* chromosomes would stem from the fact that 2L–3 first arose in an area where 2R–1 was rare or absent. Similarly it would be postulated that 2L and 2L–1 were probably attached to 2R–1 before they came in contact with 2R. The known geographical distribution of these arrangements (Carson and Stalker, 1947; Levitan, 1951a) may seem to support this hypothesis. 2L–3 is apparently not present in the Southern United States below Tennessee, an area where 2R–1 achieves its highest frequencies. North of Tennessee, 2L–3 is more common, but in the same areas 2R–1 is rare. On the other hand, 2L and 2L–1 are common in the area where 2R–1 is common. Recombination to change the associations from the original ones could occur only in females heterozygous for inversions in both arms, but in this karyotype crossing-over between the inversions is strongly suppressed (Carson, 1953; Levitan, 1953 and unpublished data). Recombination on the order of 30% or more occurs only when the females are also heterozygous for certain inversions in both arms of the X and for an inversion in the right arm of the third chromosome. Such females are very rare, attaining a frequency of 1% in few populations of the species.

Nevertheless, the hypothesis does not explain the data. For one thing, it does not account for independence with respect to 2L–2. It implies that recombination between 2L–2 and the right-arm arrangements is more frequent or of longer standing than that between 2R and 2R–1 and the other left-arm arrangements. Such assumptions are not supported by stud-

ies of recombination in wild females (unpublished) or by the probable phylogeny of the left-arm arrangements (Carson and Stalker, 1947).

The clearest evidence against the "relic of origin" hypothesis comes, however, from the absence of significant deviations from independence of left- and right-arm arrangements in the females. This shows that no matter what the modes of origin of the arrangements were, recombinations between the left-arm and right-arm arrangements have occurred often enough in the past that the number of second chromosomes with a given arrangement linked to 2R and the number with the same arrangement linked to 2R–1 can be relatively uniform. For, in the absence of selection against the new combinations, only in the closest sort of linkage can linked loci or arrangements fail to reach "populational independence." In fact, the population theory of recombination of linked loci or arrangements may be likened to the theory of mutation and back-mutation of two alleles. No matter how rare one allele is originally, if the rates of mutation and back-mutation are equal the alleles will reach an equilibrium when each is equal to 50% of the total. The pertinent rates of recombination, the amount of crossing-over under coupling and under repulsion, are usually equal, and therefore lead to equal likelihood of the combinations. Geiringer (1944 and 1948) has shown, mathematically, that the same results are to be expected when the linked loci are represented by multiple alleles in the population and when recombination is not equal in the two sexes. In a population where random association has been achieved, as between the left- and right-arm arrangements here, deviations from independence in a portion of the population must be the result of selection for certain combinations of the linked variants. Seasonal variation in these data (publication now being prepared) provides further evidence that random association is possible here and that non-random associations are due to natural selection. The seasonal results show that even in the males significant deviations from independence are confined to collections between early June and early October, such deviations being absent from flies of the overwintering generation.

It might be supposed that selection for combinations of linked arrangements occurs because genes in the two arrangements interact to form advantageous or disadvantageous phenotypes. The interaction might be simple, as in epistatic or complementary actions of genes, or it could be complex, as in polygenic coadaptation. However, such interactions lead only to individuals carrying both of the appropriate inversions being in excess, or deficient, in the population. They do not require that the interacting genes be present in the individuals on the same chromosome; they could well be on *homologous* chromosomes to give the same phenotype. Since the data show that certain linkages of the same inversions are favored over others, the effect cannot be due merly to the nature of the genes in the linked inversions, but must also (perhaps entirely) depend on the positional relationship of these genes.

The point is well illustrated by the data concerning 2L–3 and 2R–1. If the actual and expected numbers for all karyotypes with both these arrangements in table 1 are added, in each sample, the figures in the left-hand portion of table 6 are obtained. With the exception of two samples (Males and Both Sexes of Heth's Woods), the total of these karyotypes is regularly less than expected. This might give the impression that merely having 2L–3 and 2R–1 in the same individual is selectionally disadvantageous. However, chi-squares testing the significance of these deficiencies (row 9, table 3) show that in only one instance, the total sample for Crumpacker Woods, is P less than 5%. In another, Crumpacker males, P is less than 10%, greater than 5%. These results contrast considerably with those obtained when only the karyotypes containing 2L–3 *linked* with 2R–1 are

compared with expected (middle part of table 6, based on table 1 and table 3). Deficiency from expected is now found in every sample, and it is significant in five of the nine (row 10, table 3), including one, Heth males, which showed an excess over expected in the previous classification. The contrast would be even more marked if the left side of table 6 excluded types carrying 2L–3 linked to 2R–1, e.g., 3S/31. Clearly, selection against the combination 2L–3 and 2R–1 is directed primarily, if not solely, against karyotypes having both arrangements on the same chromosome. Similar results are found with repect to the combinations 2L, 2R–1 and 2L–1, 2R–1, except that in these instances the karyotypes carrying them on the same chromosome are *favored* by selection to a much greater extent than those which merely have them in the same cell.

Again the crucial karyotoypes for these conclusions are the alternative linkage types in the double heterozygotes. This points to the reason why such position effects, even if present, could not be demonstrated by previous studies of chromosomal polymorphism. These have usually consisted of egg samples exclusively. Alternative linkages cannot be detected in egg samples unless accompanied by adult analyses, and even then often lead to inconclusive results (for example, an S/1, S/1 egg from an SS/1S mother). Where adult samples have previously been run, double heterozygotes were rare (Levitan, 1951a and unpublished St. Louis data of Carson and Stalker) or absent (third chromosome arrangements of *D. pseudoobscura* studied by Dobzhansky and Levene, 1948).

How many positions effects need be postulated here? The natural population data are not clear on this point. Table 4 suggests that all the significant results of table 5 could be explained by selection against *2L–3 2R–1* chromosomes and for *2L 2R–1* and *2L–1 2R–1* chromosomes. On the other hand, the greater difference in table 4 between, say, SS/31 and S1/3S than between SS/21 and S1/2S (or 21/3S and 2S/31) suggests that there are six position effects, three adaptively advantageous (*S1*, *11*, and *3S*) and three disadvantageous (*SS*, *1S*, and *31*). SS/31, containing two negative doses, would therefore contrast more with S1/3S, two positive doses, than cases where one linkage type had only one positive and the other had one negative (*2S* and *21* being adaptively equal according to table 5).

What happens when a linkage which appears to be adaptively superior (according to the second hypothesis of the last paragraph) is combined in the same individual with the "inferior" chromosome bearing the same left-arm arrangement? The karyotypes in question are S/S, S/1; 1/1, S/1; and 3/3, S/1. Table 1 shows that the first two do not differ from expectation in any consistent way, the result expected if the effects of the chromosomes "cancelled out." The 3/3, S/1, on the other hand, are consistently deficient from expectation. Chi-squares testing 3/3, S/1 *versus* "not 3/3, S/1," each with one degree of freedom, are significant in three of the nine samples, and P is less than 10% in four others (row 11, table 3). Although they suggest that *3S* is adaptively neutral, thus contradicting part of the second hypothesis, these results may also be interpreted as meaning that *31* is "dominant" to *3S*. Moreover, in the absence of alternative linkages for the karyotype, the results could be attributable to the combination of being homozygous for 2L–3 and heterozygous for the right arm rather than to the combination of linked arrangements.

Similar ambiguities prevent use of the 2R/2R and 2R–1/2R–1 data as evidence concerning the number of position effects. For example, the excess of 3/3, S/S individuals (3S/3S in terms of linkages) in most of the samples seems to indicate that *3S* has positive adaptive value. The excess is nowhere significant, however, and is again attributable to the combina-

tion of karyotypes in the two arms. Clearer evidence concerning the number of position effects must, therefore, await the outcome of laboratory studies with these inversions.

It seems all but impossible to ascertain the genetic nature of these position effects, to determine, for example, whether they are the result of the inversions' bringing certain genes into proximity or the result merely of their making a different order of the loci. 2L–3 also causes heterochromatin which is part of the chromocenter in 2L and 2L–1 to be farther away from the genes on the right arm than in 2L and 2L–1. At the same time 2L–3 brings euchromatin which is attached to euchromatin in the other 2L arrangements into attachment with heterochromatin of the chromocenter area. However, even the position effects involving 2L–3 cannot be due entirely to the simple fact that heterochromatin and euchromatin are in certain positions relative to one another (thereby resembling the V-type effects of Lewis, 1950). They depend also on the position of the genes embraced by arrangement 2R–1. Also noteworthy is the fact that 2L–2 makes substantially similar transfers of heterochromatin and euchromatin without any apparent position effects. This difference between 2L–2 and 2L–3 also suggests that which *alleles* at the loci, rather than which loci, are in particular position is most important in determining whether a position effect occurs, for all the euchromatic loci, and many of the heterochromatic ones, in 2L–3 are also present in 2L–2. The argument is not rigid, however, for the same loci are somewhat farther from the pertinent genes of 2R and 2R–1 when they are in 2L–2 arrangement than when in 2L–3. Differences due to the breakage points also cannot be excluded (after the "structural" position effect theory of Muller, 1941, and others). Incidentally, the "structural" theory would imply that 2L–2 was the ancestral arrangement, an idea opposed to that of Carson and Stalker (1947).

Whatever the correct mechanism of these position effects they must depend on conjunct action over distances which are, relative to other known cases of position effects, very large. The minimum distance is over 10% of the euchromatic length of chromosome 2, the largest autosome. This distance would apply if the *3S* vs. *31* effects stemmed from differences in the mode of action of genes located half-way between the proximal breakage points of 2L–3 and 2R–1 because of the simultaneous presence of certain genetic material at the proximal ends of 2L–3 and 2R–1. If, as seems more likely, the position effects are due to related action of genes at the breakage points or within the various inversions, the distances must be even greater; the minimum is 21.3% of the euchromatin of 2, the distance between 2L–3 and 2R–1. The maximum distances that a locus may be from rearranged genes in order to show the position effect does not appear to have been thoroughly investigated in laboratory materials. Demerec (1940) found position effects at loci which were 50–80 bands away from the chromosome breaks, distances almost as great as the minimal one here. Baker (1954) also found position effects at loci which were quite far from the breaks, but his distances could not be estimated in terms of euchromatic salivary chromosome.

How great a role the position effects play in the adaptation of *Drosophila robusta* populations to their environment cannot be determined from the data presented here. The question will be discussed in greater detail when the rest of the material has been tabulated and evaluated. The data reported do show that the position effects are probably involved in selective differences between the two sexes (Levitan, 1951b) and in seasonal changes of the left-arm arrangements (Levitan, 1951b, 1951d and unpublished data). One implication is clear, however: an attempt to analyze the population dynamics of this species on the simple expectation that persistence of its inversions is due only to

adaptive superiority of inversion heterozygotes over inversion homozygotes must lead to puzzling results or even failure. The data show that it may be a certain *kind* of heterozygote, not the heterozygote *per se*, that is favored by selection. Some position effects seem to exert their adaptively advantageous or disadvantageous influences in structural homozygotes as well. It becomes less surprising, therefore, that no significant deviations from Hardy-Weinberg expectations seem to be found in natural populations of *D. robusta* (Levitan, 1951a, the present data (Lines 2 and 3, table 3) and unpublished data of Carson and Stalker and Levitan). In experimental populations the results often did fit an hypothesis of heterozygote superiority (Levitan, 1951a), but they did not fit it well; a recheck of the strains used indicates that one of the disturbing factors may have been the presence of 2R–1 in some of the cages, its absence from others. In *Drosophila pseudoobscura* the usual although not invariable finding has been an excess of structural heterozygotes in both natural and experimental populations (Dobzhansky and Levene, 1948; Dobzhansky, 1950). But even in this species Epling *et al.* (1953) have found that some heterozygotes are often in excess while others are not. As has been pointed out before, such findings are not crucial to the theory that persistence of inversions in natural populations depends, in the last analysis, on adaptive superiority of the inversion heterozygote. They do demonstrate though that factors which do not fit such an analysis, such as position effects described in this paper, must be considered in the proper quantitation of population genetics. Above all they underscore again the subtlety and complexity of the selectional forces in a natural population.

Summary

Data are presented concerning the gene arrangements on the left and right arms of the second chromosome in 2,160 adult *Drosophila robusta* collected over a four year period in two woods near Blacksburg, Virginia. The frequencies of structural karyotypes in each arm fit the assumption that the samples were derived from large panmictic populations. The data, particularly the flies heterozygous for arrangement in both arms, contain evidence, however, that the associations of left- and right-arm arrangements are not random. The deviations from independence are generally significant only in data from males, although the female data are often in the same direction. The hypothesis that positional differences of genes in the arrangements leads to adaptively different phenotypes, at least among the males, seems to be the only adequate explanation for the results. The position effects apparently depend on simultaneous action of widely separated genes.

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THE ROLE OF ONTOGENY IN SYSTEMATICS AND EVOLUTION [1]

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INTRODUCTION

In recent decades the basically morphological fields of ontogeny, systematics, and evolution have been brought into closer alliance by the broadly unifying concepts of genetics. Modern genetics has not only given us some understanding of the mechanisms of evolution, but also has demonstrated clearly the hereditary nature of the characteristics of all developmental periods. All growth stages and all normal developmental processes of an organism are controlled by a single genetic system and are subject to evolutionary changes. These established genetic concepts have far-reaching importance to systematics, for they provide a sound basis for the use of characters from the full range of developmental stages in classification and in the study of evolution. Research on early developmental stages has always emphasized morphology, and a vast amount of routine descriptive work is still to be done, but the value of these basic descriptive data in the solution of problems in life histories and classification has already been demonstrated on a limited scale. There is need for much wider application of ontogenetic data in such problems, and the present paper discusses some of the principles and procedures of interpretation in this field.

DEVELOPMENTAL SYSTEMATICS

The idea that developmental characters may be a source of material for evolutionary studies dates at least from the period of intense interest in descriptive embryology in the nineteenth century. Much theory and speculation have resulted, especially around the topic of recapitulation. The long popularity of this theory has somewhat overshadowed the ideas of Von Baer (see de Beer, 1951), which were essentially sound by present standards though they preceded the modern expansion of genetics. Von Baer stressed the value of comparative studies on the same growth stages of different species, rather than the search for ancestral adult characters in embryonic stages. Some of the more recent authors who have reviewed the recapitulation question and its history are Shumway (1932), Meyer (1935), Holmes (1944), and Case (1950). Additional problems of development in relation to evolution were discussed by Haldane (1932), Hubbs (1926, 1940), Waddington (1941), Gregory (1946), and de Beer (1951).

The study of taxonomy in terms of natural populations rather than of a few specimens in the laboratory is now quite standard, but there is equal need for analysis in terms of the whole ontogeny rather than of a single stage. In older taxonomic practice, notably in the vertebrates, it was generally customary to restrict study to the characters of the mature adult. Ordinarily, of course, these characters are the easiest to determine and are the most convenient base for routine taxonomic work. The life histories and early developmental stages of many groups of animals are difficult to decipher and are very incompletely known, and it is impractical to postpone a study indefinitely in the hope that all of the desired data may be forthcoming. Never-

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theless, the full characterization of a species comprises all of its genetically regulated attributes throughout its ontogeny and thus, ideally, judgment in taxonomy and evolution should be based on a unified summary of the data obtainable from the entire developmental pattern rather than on any single stage. The validity of a taxonomic judgment that is deliberately based only on the final, adult stage, when ontogenetic data are available, compares with the validity of a phylogenetic judgment that is based only on the extant species, without regard to the known fossil history of the group.

Developmental patterns differ widely in different groups of animals. Among the vertebrates, the fishes and amphibians are exceptionally favorable for combined studies in development and systematics. Although not all species of the lower vertebrates have a well-defined free-living larva, they all present developmental problems of one sort or another than can be studied to advantage by systematic methods. Development is relatively direct and uncomplicated in some fishes and amphibians. In these, growth proceeds simply and smoothly and there are few definable stages, thus relatively few opportunities for complications to arise from independent evolution of early developmental characters. But even in these species the embryonic period reveals similarities and differences in growth characteristics (in pigment cells and color pattern development, modifications of the fins, etc.) that are of taxonomic value. In most of the species, the ontogeny includes a distinct larval stage and a consequent period of metamorphosis. In these forms, the complications both in the ontogeny itself and in its evolutionary potentialities are greatly increased.

Genetics has provided a valid explanation both for the occurrence and for the limitations of independent evolution in different developmental stages. Structures that comprise the basic morphological pattern or *Bauplan* of a species are subject to extensive coordinated modifications; a major change in a basic structure (e.g., in number of somites) produces evident effects in all stages in which that structure is visibly represented. Characters that are phenotypically expressed in only one stage of development (e.g., the barbels of flyingfish larvae) can undergo evolutionary changes which alter that developmental stage but have no apparent effect on other stages (although they are, of course, carried in the genotype). Independent changes of this nature account for many well-known examples in which the larvae of two species differ more widely than do the adults, or the larvae of two obviously different species are scarcely separable. The existence of independent evolutionary changes in different stages of development emphasizes the need for study of the entire life cycle. Evolutionary interpretations that are based on fragmentary data can be equally misleading whether the specimens are adults or larvae. The wider the general background and experience in systematics, then, the more effectively ontogenetic data can be used in this field.

From the knowledge that development is genetically controlled, one can infer that the same basic evolutionary phenomena apply to early developmental characters and to adult characters. As in the adult stage, some features of the developmental pattern may be extremely stable and persistent in geologically-old phyletic lines and hence of great value as indicators of relationships. In contrast, other developmental characters may be very plastic and subject to elaborate secondary modifications and selective adjustments that have little bearing on the main lines of developmental evolution. This rather flexible evolutionary picture complicates the task of interpreting ontogeny, but it is simply another facet of variability and is a logical extrapolation from well-established evolutionary principles. Such hypotheses can be tested readily through integrated study of the characteristics of the entire ontogenetic cycle.

Patterns of Development, Larval Types

The interpretation of the relative systematic values of different ontogenetic variables is a challenging problem. In the taxonomic study of development, one attempts to distinguish between various levels of evolutionary significance in developmental characters, and to learn how environmental factors may modify the expression of these characters. The objectives and the methods are essentially the same as they are in taxonomic studies on the adult stage.

If the basic developmental pattern of a particular taxonomic group can be defined it then provides a reliable point of reference for analyzing the nature, significance, and possible mode of derivation of secondary developmental variations and adaptations in that group. Clear definition of developmental patterns and larval types that have broad phylogenetic value makes it possible to use ontogenetic characters to help determine the relationships of puzzling groups in which the adult stage is so specialized that the characters on which the taxonomist usually depends are obscured. The developmental pattern of *Sacculina* is a classic example from the invertebrates. Such knowledge also permits successful prediction of the general characteristics of development of poorly known species on the basis of known data from related species. In evolution, as in other fields, successful prediction is an important test of the validity of inferences.

Few large-scale studies on developmental systematics of the lower vertebrates have been reported, but from the results already obtained come the theoretical premises which are discussed here. For example, the complex mass of known details on the morphology and variation of frog tadpoles resolves into a simple, orderly, and conventional pattern of basic and secondary evolutionary trends (Orton, 1953). The frogs are a particularly fortunate example, for this richly varied amphibian group is small enough to be studied conveniently in its entirety, and the tadpole is an unusually distinctive type of larva and has undergone very elaborate evolutionary modifications. From these studies on a small taxonomic group come new clues that may be helpful in recognizing and defining patterns of developmental evolution in the fishes, a vastly larger and more complicated group.

Although much general descriptive work has already been published on early developmental stages of fishes, this group is so large and diversified that ontogenetic studies are still confined principally to gathering the necessary background of morphological data. This aspect of developmental study is far from completion, but it is already possible to use the available data in a wide variety of ways in the systematics of fishes. The importance of detecting and interpreting the morphological effects of direct development provides a good example.

Most evolutionary changes that modify larval characters affect the larval structures themselves, but changes that have their primary effect on egg size and yolk supply may carry secondarily a considerable alteration of embryonic and larval phenotype, that often results in the more or less extensive suppression of larval characters. In its extreme form, this is the familiar "direct development," a modification that exhibits a high degree of independent evolution in the amphibians (Lutz, 1947; Orton, 1949), and almost certainly in the fishes as well. Recognition of the occurrence and effects of direct development in the fishes is one of the preliminary steps in sorting out the various kinds of trends in developmental evolution in this vast group. The characteristics that direct development shows in the amphibians are a useful guide to help determine whether distinctive developmental characters in large-egged fishes may be correlated primarily with evolution in egg size (hence, with direct development) rather than primarily with actual evolution of larval structures.

Clues to the original or "normal" larval type in large-egged fishes may best be sought among small-egged relatives of the group in question. Three families of salmonoid fishes, the Osmeridae (true smelts), Coregonidae (whitefishes), and Salmonidae (salmons), provide an instructive example and a suggested interpretation. These fishes are closely related and indeed have often been lumped together in a single family. Typically, the smelts have small eggs and the larva (e.g., in *Mallotus villosus* and *Osmerus mordax*) has the general form, pigmentation, and compressed, transparent musculature that characterize the leptocephalus-like larva of clupeoid fishes (herrings, sardines, etc.). The salmons have large eggs and slow embryonic development, and hatch in an advanced condition followed by a prolonged yolk-bearing stage that transforms directly into the juvenile. The whitefishes have eggs of moderate size and their developmental product is intermediate between the small pelagic larva of the smelts and the large, yolk-bearing "alevin" larva of the salmons.

The salmonoids and the clupeoids, together with certain other groups of fishes, comprise the large and varied Order Isospondyli. Study of the developmental pattern of the salmons against the broad background of isospondylous fishes as a whole, suggests strongly that the well-known and widely-studied developmental characters of the salmons constitute a clear example of secondary direct development that is comparable to many such cases in the amphibians. It seems probable that the herring-like larva of the smelts is the basic larval type in the salmonoid fishes as a group, and, furthermore, that it is the normal type of larva to be expected in both the clupeoids and the salmonoids unless it is masked by secondary modifications of egg and embryonic characters. Thus, it seems apparent that the salmons skip the expected larval stage as a consequence of greatly increased yolk supply, and that the whitefishes have followed the same trend but with a less extreme result.

Larval characters that are suppressed phenotypically as a consequence of direct development are not necessarily lost genetically, but may be carried in the genotype for long periods without outward manifestation. Cornman (1943) discussed the genetics of comparable situations, with examples from problems of real or ostensible reversal of evolution. Applying this genetic background to the present problem, it can be postulated that if the Salmonidae, with direct development, gave rise to a new family of fishes in which the egg size and yolk supply were reduced and a small pelagic larval stage thus restored to the ontogeny, the genetic potentialities for the clupeoid type of larva would again find phenotypic expression, and the characters of the restored larval stage in the new group would be essentially like those of the basic clupeoid type rather than of a totally new and different type of larva.

The complexities of this example illustrate the wide scope of developmental systematics and its bearing on major evolutionary investigations in the fishes. Information on basic patterns of development and basic types of larvae in fishes should help to solve many puzzling problems at various levels, from population questions and species studies to work on the higher categories of classification.

Ontogeny and the Species Problem

In older taxonomic work, descriptions of species and the general understanding of the category of species were based on limited morphological criteria, largely or entirely from adult (or presumed adult) specimens. In modern work it has become increasingly evident that study of the species concept requires a much broader biological approach. Developmental studies contribute substantially to the solution of systematic problems at the species level, and the developmental viewpoint can help to clarify the species concept itself.

The species is the highest category that applies to "a kind" of animal; all higher levels are, by definition, group categories —groups of related kinds of organisms (see Hubbs, 1943). The species has an important and apparently very real evolutionary status. It denotes populations that have achieved sufficient uniformity in developmental pattern, in adult morphology, and in other biological characteristics, and sufficient stability in geological time, to establish and hold an area of distribution, which may become very extensive. The genetic processes that bring a population to the specific level of differentiation are probably basically similar in most groups of organisms, but these processes have different results in different groups, in respect to ontogeny and to the structures that are produced. The criteria that distinguish all species in all groups of organisms are, therefore, neither of the same nature nor of the same magnitude. Species of fishes cannot be equated exactly with species of flies or of sunflowers; species of fishes are not all separated from each other in exactly equal degree. This is apparent from comparison of adult stages of different groups of fishes, but it is even more obvious when the diverse life history patterns of groups (such as the sardines and the embiotocid fishes) are compared. Consequently, it should occasion no surprise that even though the category of species has a clear general meaning, it cannot be rigidly defined. Taxonomic categories acquire their greatest significance when they are studied in relation to the characters of particular groups of organisms (cf. Rollins' "species standard" idea, 1953), especially when these studies encompass the entire life cycle.

It is a well-known principle in taxonomy and paleontology that a given character does not necessarily confer the same categorical rank on all species that possess it. There is no universal criterion that always, automatically, denotes "species," "genus," or other category. The taxonomic value of a character depends on its stability and on the nature of its variability, and these qualities may differ greatly in different groups or even between related species in the same group. This general principle was derived chiefly from studies on mature specimens, but it is readily demonstrable in early growth stages as well, for a particular developmental character may have quite different values in different groups. Viviparity, with highly specialized embryonic modifications, is a constant family character in the Embiotocidae (surfperches), but in certain other families of fishes, e.g., the Scorpaenidae (scorpionfishes) and the Clinidae (klipfishes), some species are live-bearers and some are egg-layers. Just as species are not all precisely equivalent, neither are all characters of uniformly predictable taxonomic meaning. The significance of the characters of any growth stage must be weighted comparatively, and sound judgment in systematics therefore depends to a considerable degree on wide experience and intuitive thinking.

The flyingfishes, family Exocoetidae, afford a convenient example of the contribution of ontogeny toward solution of revisionary problems in systematics, especially problems that involve difficult questions of species definition. The literature and current classification of the flyingfishes are unusually confused; there are about 150 nominate forms, but it is probable that fewer than one-third are valid. The species are moderately variable, but for the group as a whole the total range of variation in known adult characters falls within rather narrow limits. As a consequence, some species that are clearly different, such as *Cypselurus exsiliens* and *Cypselurus heterurus*, show extensive overlap and even (in some individuals) full duplication in such characters as fin-ray and scale counts. The rigorous environment and habits of these fishes appear to favor selection toward a conservative uniformity in adult characters, and it is unusually difficult to deter-

mine not only the relationships of a given species but even what constitutes a species, if one relies solely on the adult stage. Fortunately, the ontogeny is unusually well suited for taxonomic study (Bruun, 1935; Breder, 1938; Hubbs and Kampa, 1946). The eggs and embryonic stages are large enough so that their distinctive characters are easily studied, and the larval stage shows conspicuous interspecific differences both in its special structures and in the complex sequence of its color pattern development. *Exocoetus volitans* and *Exocoetus monocirrhus,* for example, are very difficult to distinguish in the adult stage, and their synonymies are so thoroughly entangled that they probably can never be entirely clarified. Yet, the young stages of these two species are so dissimilar that they could scarcely be confused. The larval period is unusually protracted in many or most of the flyingfishes. The larger larvae have often been mistaken for adults, and a considerable number of the new names have been based on larvae, unwittingly or otherwise. Characters of species groups are especially well-defined and conspicuous in the larvae, and preliminary study suggests that phenotypic divergence in these fishes is in reality greatest prior to maturity. For an understanding of exocoetid taxonomy and interrelationships, it will be necessary to integrate data from the full range of developmental stages of each species. Indeed, for nomenclatorial as well as for biological reasons, it will be impossible to monograph this group successfully without full use of ontogenetic data. The names that were based on larvae cannot be allocated to the correct synonymy until the species to which each of these named larvae belongs is determined. A number of the larval names definitely have priority and others probably do. In the flyingfishes, and in other groups with similar problems, it is abundantly clear that accurate species diagnosis and species grouping depend on extensive knowledge of the full life cycle.

Ontogeny and the Higher Categories

Most students follow the concept that evolutionary processes operate at the lowest taxonomic levels, from species down through subspecies to unnamed races and local populations. Heavy concentration of study on these productive ranks has largely diverted attention from the higher group categories. Interest in the evolutionary significance of these higher taxonomic units is, however, a natural corollary of developmental systematics because of the necessarily broad scope of the latter field. The developmental specialist works with wide ranges of ontogenetic variability, especially if the group under study has an elaborate larval stage, for the range of difference between stages in the development of the same individual is much greater than that which separates two related species at the same stage of development. The wide interpretation of intraspecific variability that this work imposes, and the need for rather extensive concurrent study of adult characters for background, preadapt the developmental systematist to an interest in the application of ontogenetic data to some of the more inclusive problems of classification and phylogeny, such as the origin of new higher categories.

Goldschmidt (1940) and de Beer (1951) traced the historical background of a long-held, though often vaguely-expressed, idea that rapid large steps in evolution may be initiated by modifications that affect early developmental processes. This idea suggests that if a genetic modification affects the course of development only in its late stages, most of the basic anatomy is already established and only lesser (though perhaps conspicuous) details can be altered. But, if the effects of the modification are evident from the early embryo onward, there is opportunity for very extensive alterations both in the ontogeny as a whole and in the resulting adult stage. Changes of this nature could sharply increase the rate of evolution and greatly hasten the establishment of a new

bauplan. Evidence from paleontology, reviewed by Simpson (1953), indicates that the rate of evolution is commonly accelerated during the early fossil history of lines that (as we know from their later history) led to the differentiation of new higher categories.

The most extensive evolutionary results of modified ontogeny can appear in groups that have a relatively complicated developmental pattern, particularly if it includes a highly differentiated larval stage. De Beer (1951) discussed in detail the potential importance of ontogenetic changes and cited examples of various kinds of developmental modifications that might have significant evolutionary results. He treated at considerable length the idea of origin of new major groups by neoteny from highly evolved larvae. It has been speculated that even the chordates may have originated by neoteny; the notochord and somites may have been larval specializations in the ancestral stock (see Gregory, 1946, 1951; de Beer, 1951). Neoteny is, however, not the only means by which developmental modifications may have major evolutionary consequences. The entire ontogeny as a unit may shift relatively rapidly (in geological time) to a new structural plan. It has been suggested that a change of this nature, the extreme shortening of the vertebral column in both larva and adult, precipitated the origin of the frogs (Orton, 1953).

There is much evidence to support the concept of evolution of developmental processes, but Goldschmidt's extension of this topic (1940, 1952) has somewhat obscured the important basic idea. He believes not only that evolutionary modifications which affect early developmental processes can lead to new species and new higher categories but also that these modifications are of an entirely different genetic nature than those that produce new subspecies. He maintains that mutation and selection function only at the subspecific level or below, and would be too small in effect and too slow in operation to account for the production of new higher categories or even of new species. He considers subspecies to be genetic and evolutionary blind alleys that do not give rise to new species. This differs sharply from the view held by most geneticists (see Dobzhansky, 1951) and systematists that all evolutionary trends and changes of whatever level of complexity result from the same repertoire of genetic processes, and that any established population is, theoretically, a potential ancestral stock for further speciation. The hypothesis that different kinds of evolutionary processes operate at different taxonomic levels appears to hinge on insufficient consideration of the paleontological record and of the way in which taxonomic categories are used by systematists. A new higher category does not originate as such. The unit that arises in evolution is a new definable population, a new kind of animal. The initial change must take place in the genetic structure of members of a natural population, whatever the nature or direction or ultimate evolutionary consequences of that change may be. As Simpson (1953) points out, the original mutant would still be a member of the parent species. It may be helpful to compare the use of terms and ideas in this case with that in a similar situation of common occurrence in descriptive taxonomy. When a systematist "discovers a new order of fishes," what he actually discovers is a new species, i.e., a new kind of fish, that differs sufficiently from other known species of fishes to warrant, in his experienced judgement, definition of a new series of group categories up to ordinal rank to contain it.

The vast majority of new species probably evolve by means of very gradual, small changes in details of development, structure, and function—changes that conservatively keep within the framework of an established bauplan in ontogeny as well as in adult structure, and lead to new higher categories only very slowly, if at all. In contrast, new species that are produced relatively rapidly (in the geo-

logical sense) by genetic changes that profoundly affect key developmental processes, and thereby provide the morphological and functional basis for a new structural plan, are the most likely precursors of rapidly-evolving new groups that ultimately attain high categorical status. Simpson (1953) emphasizes that a major change of this nature offers new adaptive possibilities that may have a high selective advantage, and Muller (1949) stresses the probable greater importance of selective factors than of mutation rates in this kind of evolutionary situation. Since the findings of genetics indicate that heritable changes can modify the phenotype at any stage of ontogeny, genetic evolutionary change itself appears to be an example of variability over a continuous scale. The two extremes of evolutionary pattern discussed above differ in degree but not in kind, for they could be connected by a full range of intermediates.

Summary and Conclusions

Certain basic problems and principles pertaining to the role of ontogeny in systematics and evolution are reviewed, and their application to the fishes is discussed. In recent years the unifying principle of genetic inheritance has drawn these fields closer together. Demonstration of the genetic nature of developmental characters, hence their validity as evolutionary material, is particularly important. The same basic principles of evolution apply to the adult stage and to earlier stages of development. Characters that are unique to particular developmental stages in the same species can evolve independently, and these independent trends show that reliance on fragmentary data from any single stage in ontogeny can be equally misleading in taxonomy. Carefully coordinated study of the entire ontogeny of each species is, therefore, greatly needed.

A key problem in developmental systematics concerns the distinction between various levels of evolutionary significance in different developmental characters, and we are guided toward its solution by the well-established principles derived from studies on adult stages of organisms. Data on basic developmental patterns and basic larval types of major groups can help to solve taxonomic problems at all levels. These basic developmental criteria provide reliable points of reference for interpreting complex secondary trends, and aid in making taxonomic decisions when the adult characters are too specialized to be dependable indicators of relationships.

The developmental approach to systematics also helps to clarify the species concept, for certain of the basic difficulties of the latter are best understood in terms of a broad, ontogenetic species definition. The very unequal degrees of difference between species, and the variable taxonomic value of the same character in different groups of species, gain clarity from the wider perspective of developmental study. The flyingfishes provide an outstanding example of the importance of developmental work in the untangling of difficult taxonomic groups.

Ontogeny also contributes toward understanding the origin and evolution of higher categories. It has long been held that geologically-rapid, major evolutionary progress can result from genetic changes that affect key developmental processes, especially in groups that have a complicated life cycle. A new structural plan can evolve by neoteny or by coordinated changes that alter both the adult and the early stages. New species that result from such rapid and drastic developmental evolution are more likely to lead to establishment of new higher categories than are new species that are produced much more slowly by selection of very small mutations. These two extremes of difference in species formation can be connected by a full range of intermediates, and there is no need to postulate, as Goldschmidt did, separate kinds of genetic processes for the evolution of different categories.

Integrated studies on the entire devel-

opmental pattern can be a great stimulus to achievement in the fields of systematics and phylogeny, and should bring us closer to a real understanding of the interrelationships and evolution of living organisms.

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EVOLUTION IN THE NOTOSTRACA

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The Notostraca are phyllopod Crustacea in which the carapace is shield-shaped and covers the anterior part of the body; together with other phyllopods, they are considered to be relatively unevolved Crustacea—there is a high, but irregular, number of appendages (forty to sixty pairs are usual) and the segmentation of the body is anameristic.

It is characteristic of phyllopods that they occur in temporary rain pools, generally in arid or steppe country where such pools are common, and are unable to maintain themselves in the face of competition from higher Crustacea or Insecta (Ardö, 1947).

The survival of such primitive and vulnerable animals poses an interesting problem—the key to which may lie in their main adaptation to a temporary habitat, the drought-resistant egg. The possession of such an egg, from which hatching normally occurs only after desiccation, is an obvious prerequisite for the exploitation of a temporary fresh-water habitat by a group of animals which do not have the capacities of aerial migration which the Insects possess.

These drought-resistant eggs of phyllopods are the only possible means of dispersal for the group, for the pools in which the animals occur are isolated from one another, and are only rarely part of a stream system along which dispersal of adults would be possible.

The eggs are small, light in weight because of their dry alveolar shells, and are sticky when laid in at least one genus (*Triops*, Notostraca); further, the eggs of some Anostraca are known to retain viability after passing through the guts of Amphibia (Mathias, 1937). These facts suggest several possible means of dispersal—in or upon larger animals, attached to dry pieces of wind-blown vegetation, or airborne singly in wind currents (a desert dust-devil will whirl particles much denser than the eggs of phyllopods high into the air).

That these passive means of dispersal are effective is quite clearly shown by the ubiquitous occurrence of phyllopods in suitable pools wherever these occur. Notostraca occur on such isolated oceanic islands as the Hawaiian group, and in the few suitable pools that the rainy English climate permits. The phyllopods show another characteristic of passively distributed invertebrates—that of very widely spread, sometimes almost cosmopolitan species; in a recent study of the Notostraca for a systematic revision I found that *Triops longicaudatus*, which Linder (1952) showed was the only species of the genus in the Americas, extends from the West Indies through Central America and right across the Pacific to Japan by way of the Galapagoes, Oahu and New Caledonia. In all this area there is virtually no morphological change (Longhurst, 1955).

These facts of dispersal and geographical distribution seem to me to explain the survival of the phyllopods. The initial arthropod invasion of temporary pools may well have been performed by the primitive fresh-water Crustacean fauna and has radiated into the forms of phyllopods we see today—the carnivorous Notostraca, the "pelagic" Anostraca, and the burrowing, detritus-feeding Conchostraca. This early fauna would have spread and occupied at least a high proportion of the suitable pools, and such a cosmopolitan occupation would have effectively prevented any geographically iso-

lated, phyllopod-free, part of the environment from forming a place in which later, more highly evolved forms could have adapted themselves to life in temporary waters.

This is in line with modern theories concerning the primary importance of geographical isolation in, at least, speciation and adaptive radiation. The small amount of essential adaptation—drought-resistant eggs and a rapid rate of growth—would surely have been evolved in, say, Amphipods or Isopods if some such prohibitive factor were not operating. Here the essential adaptation to the unusual habitat seems to have enabled the pioneer arthropods to have retained possession of the habitat.

The lack of competition and the unchanging nature of the habitat would have produced no selection forces for further evolution in these phyllopods, and they have retained a primitive, unevolved form in consequence.

Fossil Notostraca are, unfortunately, sparse, but Guthorl (1934) illustrates what are certainly carapaces of these animals from the Permian deposits, although it is not possible to relate these to either of the modern genera. Trusheim (1938) found abundant remains of Notostraca in European Triassic material, and his figures leave no doubt that these forms were quite remarkably like one of the extant species; they were well preserved and Trusheim was able to make out details of the armature of spines on the exoskeleton—these are identical with those of *Triops cancriformis* except that the terminal spine on the dorsal carina was relatively small in the Triassic animals; I should consider these two forms to be conspecific if they both occurred today. *Lepidurus stormbergensis* (Barnard, 1929) from the Upper Triassic of South Africa is almost indistinguishable from some specimens of extant *L. arcticus* as far as one can see from Barnard's figures.

The systematics of the Notostraca accords very well with my hypothesis of their survival. There are only two genera, *Triops* and *Lepidurus*, each with a small number of very wide-spread species, as if the geographical barriers which are essential to speciation in less passively distributed animals are ineffective in the face of the efficient dispersal of the resting eggs.

Although Notostraca are normally characteristic of pools in arid regions, one species—*Lepidurus arcticus*—occurs only in the circumpolar arctic regions, where it lives in large lakes, stream systems and small permanent or temporary pools; possibly this is a case where adaptation to one habitat—desert pools—in which there is a premium upon rapid development and reproduction may have preadapted the animals to another, completely different, environment where conditions amicable to life occur seasonally for similarly short periods.

Some Anostraca exploit the period in very early spring when the temperature begins to rise, but before the predatory insects are active—*Branchipus vernalis* occurs in permanent pools in North America and is active only in this very short period at the end of winter; it then lays eggs which lie dormant until the same time in the following year, when they hatch and develop very rapidly before the pond arthropods generally are active. This is a way of life which is a conceivable step in the evolution of *Lepidurus arcticus* from a temporary pool animal to an inhabitant of boreal lakes.

There is some evidence that in *Triops* hermaphrodite reproduction is correlated with range extension; in *T. cancriformis* the European and North African populations fall into three categories—bisexual in the south, irregular occurrence of males in central Europe, and hermaphroditism in the north (Longhurst, 1954, 1955). During the glacial period the whole of Europe would have been untenable for all Notostraca except *Lepidurus arcticus* (which is known to have occurred in Britain at this time) and it may be that the post-glacial extension of *Triops cancriformis* from the refuges was performed by

hermaphrodites, which have the advantage that only a single egg is neccessary to effect a successful colonization, which must make lodgements very much more likely. Perhaps the sporadic male occurrence in central Europe reflects a spread to the north of bisexuality. The same species occurs in rice fields in Spain, the Carmargue, and North Italy and here the populations are composed, as far as present records show, entirely of hermaphrodites. Perhaps this is another case of a newly available habitat being colonized first by hermaphrodites.

Triops longicaudatus in North America is bisexual over most of its range, but in the Californian rice-fields no males occur (Rosenberg, 1947) and all the individuals present appear to be hermaphrodites (Longhurst, 1954). It may be significant that no males have been found in any of the outlying populations on the Pacific islands or Japan—although Linder (1952) examined hundreds of individuals from the Galapagoes, and Uéno (1927) 73 from south-east Japan. (The samples that I have seen from Oahu and New Caledonia, though small, contain no males.) This may be the result of another range extension from a central mass of population in America.

It must be emphasised that much of this account is, of course, hypothesis; but the survival of a very primitive Crustacean which is apparantly in a state of evolutionary stagnation calls for some attempt at explanation. The survival of 'living fossils' is not explicable by any general theory, but each case must be considered individually; the survival of Notostraca appears to be due to causes which are diametrically opposite to those which operated in the case of *Sphenodon*, in which the important factor was probably complete geoggraphical isolation on a remote land mass.

Summary

The Notostraca have a passive means of dispersal, so effective as to enable them to occupy suitable temporary pools wherever they occur—even on remote oceanic islands. They are apparently in evolutionary stagnation.

Their method of dispersal may account for the survival of such primitive Crustacea, for they would have at all times fully occupied their habitat, leaving no geographically isolated, notostracan-free part of it in which later evolved forms could have adapted themselves to life in temporary pools. This is in accordance with modern theories of the paramount importance of geographical isolation in evolution.

It is suggested that life in temporary pools may have preadapted Notostraca to life in the arctic, where the growth period is similarly curtailed.

Hermaphroditism occurs in some species of Notostraca, and there is some evidence to show that this method of reproduction may be associated with range extension.

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THE PROBLEM OF EXTINCTION, WITH SPECIAL REFERENCE TO AUSTRALIAN MARSUPIALS

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The extinction of established species is no better understood than the emergence of new ones. This paper presents a brief discussion of reasons commonly given for the extinction of species of vertebrates, with an expression of some of the difficulties that arise in applying these ideas to Australian marsupials. Some comments are made on psychological and physiological characters of vertebrates in relation to extinction.

GIGANTISM

Much has been written about the gigantism of certain Pleistocene species, the advantages in a cold climate of greater body mass per unit of body surface for the conservation of calories, and the disadvantages of large size when the Ice Age had passed. An evaluation of the phenomenon of gigantism needs to take into account the following considerations:

1. Giants existed in the warmer Tertiary period, e.g., elephants. There were giant Tertiary mammals in the isolated Australian continent as in the interconnected continents (Gill 1953*a*). Many giants are still living, such as horses, giraffes, camels, the rhinoceros, and elephants. Gigantism is by no means limited to the Pleistocene, nor to the mammals. Conditions were satisfactory for some giant mammals in the Tertiary, many in the Pleistocene, and some now.

2. Half of the Ice Age consisted of warm interglacials when conservation of calories was of no value and could be a real disadvantage. The glacial and interglacial periods of the Quaternary may be expressed by a damped harmonic curve, and we are now in the quick small changes at the end of the curve. The Quaternary fauna therefore had to accommodate itself to warmer as well as colder times, and in the past 25,000 years these changes have been very rapid. In Victoria about 12,000 years ago there was a pluvial period, followed by the Arid Period (= "Climatic Optimum" of Europe and the "Postglacial Thermal Maximum" of North America), followed by another pluvial. There is evidence that the movement is toward the arid again. The fauna has thus had to adjust itself to very rapid changes. This could well have contributed to extinction in certain cases and places. In the past 12,000 years approximately, *Diprotodon, Nototherium, Palorchestes, Procoptodon,* giant *Macropus, Thylacoleo, Thylacinus,* and *Sarcophilus* have died out in Victoria, and indeed in the whole of Australia except for the last two which still survive in Tasmania. The present is altogether atypical of geological time as a whole. The world was never more changing than in the Quaternary, and never more in the Quaternary apparently than in the past 25,000 years. The world was never more diverse in landscape, and therefore never with more ecological settings, and opportunities for ecological isolation. "We are now in the tail end of an ice age and living in a period of crustal and climatic violence as great as any the earth has known" (Russell 1941).

3. Gigantism is a universal phenomenon, appearing as much in geographically isolated Australia as in Eurasia. No local factor or factors are therefore likely to be the cause, but rather some worldwide effect. Likewise, the tendency for Quaternary giants to become extinct has oper-

ated in Australia among the marsupials as it has on other continents among the placentals. The chief causes are therefore not connected with the internal economy of one group of mammals.

4. An effort is being made to discover what Australian marsupials were alive in which subdivisions of the Quaternary, and what their relative abundance. An estimate of relative sizes of populations is gained from the number of individuals represented in fossil collections from a given natural area. In the late Pleistocene, for example, the *Macropus titan* gens was dominant while *Macropus canguru* (a related living species) was comparatively small in numbers, but in the interval *M. titan* has become extinct, and *M. canguru* has become the dominant species in the same area (the plains of Western Victoria).

5. Some giants, like *Diprotodon,* survived for a very short time (as far as present knowledge shows us), while others, like *Nototherium,* continued in strength from the Tertiary to the close of the Pleistocene (see Gill, 1954, pp. 27–28). *Diprotodon* appears to be a more specialized and larger congener of *Nototherium,* and it may be that the more specialized forms did not last so long as the less specialized in the quickly changing conditions of the Quaternary.

6. What is involved in the abstraction "gigantism"? There are *physical factors,* such as the support and locomotion of such large masses of protein, etc. There are *physiological factors,* such as the maintenance of such large masses of living tissue. For herbivores particularly, this means ingesting great quantities of food, which involves power of locomotion to get to the food, and adequate buccal equipment for handling these quantities. On the physiological side too is the important matter of heat gain and loss. There are *statistical factors* also, such as the smaller number of giant individuals than small ones which can be maintained on a given food supply. Under those conditions the size of the breeding population is reduced. A smaller population means fewer gene combinations and so a limitation on selection. Finally, there are *psychological factors,* such as the sense of security a larger animal has in the presence of smaller predators. A thylacine would attack a sheep, but it is hard to imagine a thylacine attacking a healthy adult *Diprotodon.*

Gigantism *per se* cannot be the sole cause of extinction, because giants existed before the Pleistocene, and some exist still. Perhaps some of the concomitants of gigantism (such as the factors outlined above) had a powerful effect. It seems wiser at this stage of our knowledge to seek the cause of extinction of each individual species, rather than some single universal factor.

Climatic Change

This is another of the classic causes given for the extinction of Pleistocene giant species. Gregory referred to the remains of extinct Australian marsupials from the Darling Downs in Queensland, and commented, "It seems most probable that their extinction resulted from a gradual change of climate and more effectual drainage through the deepening of the watercourses."

1. Some have regarded the mid-Holocene Arid Period of Australia as the cause of extinction of the Diprotodontidae, but the family goes back to the Tertiary (Gill, 1953*a*). Diprotodontids survived the tropical to sub-tropical conditions of the Tertiary and the warmth of the Interglacials which no doubt were quite as hot as the Arid Period. Lack of water cannot explain the event, because although some areas became arid, others had an adequate rainfall. The family possessed powers of migration equal to keeping up with moving climatic belts because it spread all over the Australian mainland and into New Guinea and Tasmania. There was no physical barrier to prevent their migration, in that the Great Dividing Range of Eastern Australia

runs in general north and south. *Diprotodon,* the largest and heaviest member of the family, is found at all elevations from sea-level to over 2,000 feet in mountainous country (e.g., Omeo, Victoria). However, the whole family died out despite ability to migrate, and the presence of a large area in which to escape disagreeable climatic conditions. Both the large *Diprotodon optatum* and the smaller *D. minor, Nototherium,* and *Euryzygoma* died out. Genera that had ranged from the Tertiary perished as well as those of more recent development. Darwin pointed out (1884, pp. 85–89) that luxuriant vegetation is not necessary for the survival of large animals because in Africa today many large animals live in dry areas.

2. There are instances of marsupials dying out on the mainland of Australia but surviving on islands off the coast. Woodward (1909) instances Barrow Island, Western Australia, where four species of mammals and one of birds lived on but were extinct on the mainland. Climatic change on its own could hardly account for this phenomenon. The absence from the island of some factor operative on the mainland seems to be indicated.

Emergence of Man

Yet another factor suggested to be of importance in the extinction of the giant Pleistocene mammals is the emergence of man as a numerous and widespread member of faunas. Possession of comparatively high intelligence, and the invention of weapons, greatly extended his power in proportion to his size and strength, transmuting him into the predator *par excellence.* Sir Richard Owen, the great anatomist, drew attention to this in 1861 (p. 438). As an example of a modern author we may quote Romer, who says, "The spreading of mankind, *Homo sapiens,* is the only new feature in the late Pleistocene. Man may perhaps be responsible in some degree for this catastrophe; but his influence at the most must have been an indirect one." Le Souef (1884, p. 756) made this same suggestion relative to the Australian extinct marsupials, commenting, "They no doubt fell an easy prey to the blackfellow's spear, as they were clumsier and less agile than their descendants." The presence of the aborigines was a factor of importance (Gill, 1953*b*, pp. 59–61), but the same cannot be said concerning the lack of agility of these animals. Small agile species have become extinct as well as the large slower animals. In any case, the hunting methods of the present Australian aborigines, and presumably those of the past, do not involve the agility of the animal. A master of camouflage, the aborigine approaches within spearing distance of a kangaroo or wallaby without being detected. His quarry is usually at rest when he spears it. The selective factor for the survival of the animal in the presence of the aborigine is therefore not agility but alertness—a physiological and psychological factor. Moreover, the aborigines did not kill for killing's sake, but had an awareness of the need to conserve their food supply. These facts suggest that for these animals to die out there must have been at work factors other than the presence of the aborigines.

Europeans are often blamed for the virtual extinction of the Tasmanian Wolf, *Thylacinus cynocephalus,* but they really only speeded up a process already in operation (Gill, 1953*c*). Some species of *Thylacinus* were already extinct altogether, and *T. cynocephalus* was extinct on the mainland when Europeans first came to the country.

The Dingo

The dingo is sometimes blamed for the extinction of the giant marsupials in Australia. It is pointed out that it is a more efficient kind of mammal than the marsupial carnivores, i.e., a placental, and also that it is more daring than the thylacine. However, the giant marsupials died out in Tasmania where there is no dingo just

as they did on the mainland where it is present. Harper's view (1945) is that "an apparently minor predatory role is played by the dingo (*Canis dingo*), which was presumably introduced by aboriginal man." It is generally accepted now that the mainland aborigines brought the dingo to Australia with them (see Gill, 1953*b*), and if this is so, then two new factors came into play at once on the Australian fauna—the aborigine, and his dog, the dingo.

Psychological Aspects

There is in the literature little serious discussion of the temperament (a function of the endocrinological system) and psychology (mental structure) of species of mammals in relation to survival and extinction. Some ideas are discussed below and for convenience the term "psychology" is used to include temperament.

1. The psychological aspect of survival was first made vivid to the writer by the following experience. When on holiday in the country, a farmer friend asked for assistance to extricate a valuable cow that had become deeply bogged in a nearby creek. We tried to urge the cow out, but it just would not help itself. So the farmer fixed one end of a piece of thick fencing wire to a tree, and the other round the horns of the cow. Then he tightened the wire with a fence strainer until the cow's neck was stretched to an alarming degree. Still the cow would not try to extricate itself. "That's the trouble with these highly bred animals," commented the farmer, "they have no morale. They give in far too easily." Eventually we got the cow from the creek, but under normal conditions it certainly would have perished, although physically this was not necessary. If possessed of sufficient "morale," the cow could have extricated itself, and indeed might never have got into that predicament. Many animals (including humans) perish by reason of psychological characters of this kind. Certain psychological characters mark certain species of Australian marsupials, and these characters must have an effect on survival and extinction.

Of value in this connection are the long and careful observations in the uninhabited country of Western Tasmania by Weindorfer and Francis (1920). These authors relate, for example, the important psychological difference between Bennett's Wallaby [1] (which they refer to below as a kangaroo), and the Rufus-bellied Wallaby.[2] "Whereas the latter is capable of using its senses in times of danger, and often successfully extricating itself from a snare, the former exhibits its mental inferiority by almost invariably falling a victim. Reference has been made to the tracks which kangaroos and wallabies alike use when moving from one place to another. In doing so, the animal's body is not only just bent forward, but its front quarters are actually carried somewhat lower than its rump. Should a kangaroo happen to place its head and neck into the fatal loop of the wire necker, its life must end there and then, for as soon as the wire, by the forward movement of the animal, begins to tighten, there is a mad leap for liberty by the doomed animal, which lands it, in most cases, full length on the ground with a broken neck, or, if this does not happen, it will choke itself in its frantic endeavour to escape. How different under such circumstances does the far smaller wallaby behave! There is no mad rush to escape in its case, but with almost human-like intelligence it tries to remove the inconvenient encumbrance with its front paws, leaving sometimes a little tuft of fur attached to the wire." The quiet care with which the wallaby escapes from the traps might suggest that it is a placid animal unsuited for preserving itself in combat, but the opposite is actually the case. "It is an intensely quarrelsome animal, as is evidenced by the frequently scarred con-

[1] Now called the Brush or Red-necked Wallaby, i.e., *Wallabia rufogrisea* Desmarest 1817.

[2] Now called the Tasmanian or Red-bellied Pademelon, i.e., *Thylogale billardieri* Desmarest 1822.

dition of its skin, and its pugnacity spoils the pelt from the trapper's and the skin-dealer's point of view. It is, of course, weaker than the average hunting dog, but nevertheless puts up a good fight, using both hind and front feet, and accompanying its efforts with an angry growling."

The authors state that "The wombat would seem to rival the cat in its tenacity of life, and still makes efforts to escape even after experiencing the severest injuries."

Referring to the possums, Weindorfer and Francis say that "The Ring-tail has, as enemies, the Native and the Tiger Cat, from which it may escape by taking to a tree, where, in turn, it may be attacked by birds of the owl family. So used is the Ring-tail to these enemies that it does not seem to comprehend any other danger, and therefore falls an easy prey to the gun."

The Tasmanian Phalanger, *Trichosurus vulpecula* var. *fuliginosus*, "is the most inquisitive of animals. Everything unusual must be inspected by it. . . . It is no fighter, though endowed with formidable claws and a strong set of teeth." On the other hand, the Tiger Cat, *Dasyurus maculatus*, is "one of the pluckiest animals of the bush, and will fight for its life to a finish." It has a "cautious nature." In contrast is the closely related Common Native Cat, *Dasyurus viverrinus*, which "is far less cautious and suspicious." Further helpful notes are given on the natural history of these species by Kershaw (1952).

The above interesting observations by Weindorfer and Francis describe psychological characters which could be of importance for survival, but which could not be inferred from those parts of the animals that are preserved fossil. In fact, wrong conclusions could be reached from structures alone, in that the phalanger with the formidable claws and strong teeth suggesting pugnacity was in fact no fighter at all.

2. Some animals are psychologically very resilient and accommodate themselves readily to changes in their environment, whereas others are adversely affected by change, suffering a kind of depression. This may be illustrated by the fact that when in the early days Tasmanian devils (*Sarcophilus*) and Tasmanian wolves (*Thylacinus*) were often shipped to the mainland, the former stood captivity and transport without difficulty, whereas the latter wilted under these circumstances (Gill, 1953*c*, p. 88). The thylacines generally did not last long in capitvity, even in Tasmania itself.

Another illustration of the varying power of adaptation of Australian marsupials, is seen in the fact that as the country is settled, most of the species die out locally, but not the possums. They are to be found everywhere—in city parks, in suburban gardens, in country barns, in village halls—and can be a real nuisance. This psychological resilience of the possums must be an important survival factor, and one which of course can never be discovered by an examination of the animal's bones, which is all that remains of extinct species. It is interesting to note that possums have persisted right through marsupial history. As Simpson (1930) has pointed out, they have changed least of all the marsupials, and perhaps of all known mammals.

Animal Odors

Yet another factor that may be of value in survival but which would be missed by a palaeontologist examining an extinct animal's bones is that of animal odor. For instance, it has been reported repeatedly that when dogs picked up the scent of the Tasmanian thylacine, they were manifestly upset, moving close to their owner and whimpering. Horses reacted somewhat similarly. The animal's scent somehow engendered fear. Its scent was a protection, and therefore a help in survival.

Conclusions

1. Numerous species of Australian marsupials have become extinct during the

Quaternary, but we do not know why. No single reason given appears adequate to explain the process. It seems to the writer that no simple view of extinction is sufficient, and that the reasons are probably complex. Also there is evidence to suggest that what caused the extinction of one species may not have been operative in another, although there were worldwide factors. It appears advisable to study the extinction of each species separately.

2. Besides the physical characters which we can deduce from the fossil remains of these animals, there would be other factors of a psychological and physiological nature which we will never be able to determine accurately. We find guidance only in analogy. Illustrations of these factors are provided from surviving Australian marsupials.

3. The very adaptable possums have survived from the Cretaceous to the present in America, and from at least the Oligocene to the present in Australia. Australian possums readily adapt themselves even to the urbanisation of their former haunts.

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NOTES AND COMMENTS

THE EFFECT OF A YEAST UPON THE INCORPORATION OF PHOSPHORUS INTO THE TISSUE OF ADULT FRUIT FLIES[1]

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It is known from previous work (King, 1954) that phosphorus uptake by *Drosophila melanogaster* is increased by the presence of *Saccharomyces cerevisiae*. However, in the earlier work it was not possible to calculate the absolute amount of exogenous phosphorus (phosphorus from a source external to the fly at time zero) incorporated into fly tissue. In the present work the total exogenous phosphorus content of a fly sample can be calculated from a knowledge of the radioactivity of the sample and the specific activity of the pool which supplies phosphorus to the yeast population (cf. King and Wilson, 1954, for further discussion).

MATERIAL AND METHODS

A solid synthetic medium ("Medium A," King and Wilson, 1954) was used which allowed optimal growth of *Saccharomyces cerevisiae*. The medium, however, did not contain all the factors necessary for *Drosophila* growth. The phosphorus content of Medium A (0.226 mg P/g wet weight) falls within the range of the phosphorus contents of most fruits. Yeast grown on Medium A contained 5.546 mg P/g wet weight.

At time zero twenty-five pairs of 0-1 day old *Drosophila melanogaster* males and females (Yale-Canton-S strain) were let feed for one day upon 50 cc of the solid synthetic medium containing one P^{32} atom/1×10^8 P^{31} atoms. The radiophosphorus was supplied by the Oak Ridge National Laboratory at Oak Ridge, Tennessee. Half-pint milk bottles served as culture containers. Two such cultures were started differing only in that the surface of one was covered with *Saccharomyces cerevisiae*, while the other was sterile. The yeast colony had developed from a single drop of labeled yeast suspension added three days prior to T_0. Incubation for the yeast had been at 30° C. The flies were kept at 25° C. Following the treatment the flies were removed and weighed in groups of ten. Each sample of ten flies was ashed, assayed for radioactivity and the exogenous phosphorus content per mg wet weight calculated.

[1] Research carried out at Brookhaven National Laboratory under the auspices of the U. S. Atomic Energy Commission.

RESULTS

The results are given in table 1. The data show that under the conditions of the experiment twice as much exogenous phosphorus is found in flies fed on yeasted medium as in those fed on unyeasted medium. Females fed on yeasted and non-yeasted medium are found to contain, respectively, 1.3 and 1.5 times as much exogenous phosphorus per unit weight as males. Females fed upon yeasted medium weigh 1.4 times as much as females fed upon non-yeasted medium.

TABLE 1. *The effect of yeast upon phosphorus uptake by flies*

		Avg. weight (mg) following treatment	Exogenous P (μg) / Wet weight (mg)
Yeasted series	Males	0.83	1.54
	Females	1.56	2.07
Non-yeasted series	Males	0.78	0.76
	Females	1.13	1.11

DISCUSSION AND CONCLUSIONS

Assuming the same fraction of the ingested phosphorus is incorporated into tissue in each case and that flies on yeasted medium get the major portion of their phosphorus from yeast, the insects on non-yeasted medium must ingest ten times as much food as those on yeasted medium to account for the amount of radiophosphorus found in the flies of the two series.

The above experiment demonstrates the ability of yeasts through their multiplication upon a suitable substratum to increase the availability of phosphorus to an insect feeding upon the same substratum and, as a consequence, to increase the rate of phosphorus uptake by the insect. It is reasonable to assume this phenomenon is widespread in its occurrence. The availability of phosphorus is in many cases the limiting factor deciding the amount of life a given substratum can support. These considerations taken together may partially explain the origin and

the adaptive significance of the many elaborate anatomical devices and behavioral patterns found among insects which insure maintenance of a continuing association with various species of yeast (cf. Chatton (1913), Buchner (1930), Brues (1946), and Steinhaus (1947)). Once an association between an insect species and a yeast has developed, the insect could lose without danger the ability to synthesize compounds abundant in the yeast. Thus, in a stepwise fashion the insect would become dependent secondarily upon the microorganism for the supply of numerous growth factors. The importance of yeasts in supplying growth factors to insects is well documented (cf. Wagner, 1944, 1949).

SUMMARY

Adult *Drosophila melanogaster* feeding upon a synthetic medium incorporate larger amounts of exogenous phosphorus into tissue, if the medium contains live yeast (*Saccharomyces cerevisiae*). Insects on non-yeasted medium must ingest ten times as much food as those on yeasted medium to account for their observed exogenous phosphorus contents. This being the case, it is suggested that the association of many insects with yeasts may have originated to insure efficient utilization of the phosphorus of the environment.

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THE GENESIS OF MAN [1]

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Man, in his emergence, acquired one of the cruellest and most generous endownments ever given to a species of life by a mysterious and mischievous providence. For thereby a life form arose denuded of the innate reflex instincts which, tried and tested through millions of years of biological experience, constitute each form's most precious inheritance. No other species comes into the world with so few fixed reactions for survival, knows less inherently how to maintain itself. In no other form of life are the instincts so malleable, so changeable in object, so easy to reverse into their opposites. In what other species than man could self-flagellation create a feeling of well-being, celibacy and castration become a means of ensuring immortality?

Along with this deficiency in innate, individual survival instincts, nature has endowed man prodigiously with an apparatus which has enabled him to become her competitor and lately in many spheres her master. Man's control over nature arises out of his unique powers to register, analyze, and synthesize into techniques the phenomena of the external world. By virtue of the fact that he can form ideas out of experience and can transform the ideas in his mind into hypotheses and experimental procedures he has been able to insinuate his will into the mighty and awesome processes of nature. This power, even if only in fantasy as in previous epochs, has caused man to identify himself in direct descent with the gods with whom he has associated the powers of nature.

This strange paradox, which has come into sharp and dangerous focus with the triumphs of modern technology, has been commented upon by many observers and thinkers. Breasted has stated the matter succinctly as follows: ". . . man is morally still a mere child playing in a nursery full of the most dangerous toys. . . ."

[1] Reprinted from The International Journal of Psycho-Analysis, 34, 1953, pt. 2, 1–7, with permission of the Editor, W. Hoffer, M.D.

In psychiatric terms man is an idiot genius; in neurological terms a motor god with a sensory defect; a gigantic technological intelligence attached to midget social intelligence, similar to the mammoth dinosaurs.

One of the main reasons for this social idiocy is that man's mental apparatus is primarily designed for perception of the external world of things and poorly equipped for the perception and understanding of the world of persons. Proof of this deficiency, which many do not like to admit, is the fact that the discovery of the unconscious, an achievement requiring no special instruments or prior scientific advance, came only about some fifty years ago. If the reactions of the human mind were as well understood as the reactions of inert substances, man's powers of destruction could begin to be brought under control. A crucial missing link in man's knowledge of man is the unsolved problem of how he came into existence.

Man's descent from an ape-like creature is the only fully established fact of his genesis. Insight into how the transformation from pre-human primate into man came about is completely lacking. The profound importance of earlier stages of development in determining structure and functioning of higher and more mature organisms has been firmly established by the studies of embryology, neurology, and comparative anatomy as well as by the monumental researches of Freud. The past or history of each organism as well as species is the major determinant of how and why the individual or life form operates. Therefore insight into the evolution of man, a process still in a state of flux, is of crucial importance for the critically needed understanding of man by man.

The primary innate characteristic of man, permeating all his behaviour to the dismay of the theologian and philosopher, is that he is inevitably and eternally a very loyal subject within the animal kingdom. As an animal, man primarily "lives by consuming other living things alone," is thereby endowed with instincts, mental traits, and anatomical structures for killing and consuming other forms of life. As an animal, man is eternally doomed to parasitism on other life forms, and as a successful and dominant animal species the intensity of his aggressive instinct and the skill he has in instrumenting it make him the king of the tooth and claw kingdom. What other animal form than man could be induced to partake in the horrors, the biological shock of modern war?

Secondly, man belongs to the class mammalia, and in this regard as well is no second-class citizen. It should be remembered that mammalianism developed on the basis of the intensification of the sexual instincts, so that body areas such as the mouth of the infant and the breast of the female as well as the genitals (as with non-mammals) became erotized. In a mammal all senses can become suffused with erotic sensation; smell, touch, and taste as well as sight and hearing. In this regard too, man is distinguished by a greater intensity of instinctual drive as demonstrated by his constant, non-cyclical sexual interest. In this connection the validity and importance of Freud's description of the libido should occasion surprise and disbelief only to those invertebrates in whom reproduction is a mechanical reflex act devoid of manifest sensuality.

Thirdly, man is a member of the order Primates, sub-order Anthropoidea, infraorder Catarrhini. These distinctive patents of nobility have left a heritage of fearfulness, manual dexterity, and foveal vision. For the primates are primarily herbivorous arboreal animals, results of an evolutionary trend which consisted in taking to the trees in flight from the dangers of other large animal forms. With this they renounced the carnivore's combativeness and delight in blood and flesh in favor of a safer vegetarianism. Man's manual dexterity is derived from the brachiation necessary for living in the trees, and this retreat from a more aggressive existence on the land developed also another basic function, that of foveal vision.

The emergence of the stock from whence man arose is generally timed as having occurred during the Pliocene epoch of the Caenozoic period or over one million years ago. During the succeeding Pleistocene epoch or the period of glaciation, distinctly pre-human forms such as *Sinanthropus* and *Pithecanthropus* developed about 500,000 years ago. Neanderthal man has been placed as emerging about 200,000 and Cro-Magnon man about 25,000 years ago. At this latter period skeletons of *Homo sapiens* first appear, and since this time there has been skeletally no alteration in man.

The pre-humans from whence man originates demonstrate in their emergence distinct behavioural changes from their simian ancestry. Discarding their arboreal, defensive habits and herbivorous diet, the early pre-humans became terrestrial, aggressive, and omnivorous. There is definite evidence that *Sinanthropus* was a flesh-eater, unlike the other higher primates (gorilla, chimpanzee, orang-utan, gibbon) which are herbivorous. The adoption of a terrestrial habitat freed the upper limbs from locomotion and permitted the final improvement in manual dexterity which found its expression in the eoliths and stone tools and weapons of the Old Stone Age. Instead of the upper limbs being used for locomotion, the hands became an instrument focusing the increasing aggressiveness of emergent man into tool and weapon making and the control and manipulation of fire.

In other words the emergence of pre-humans was characterized by a marked resurgence of

aggressiveness in one of the anthropoid stocks. The inherent aggressiveness of animalism became greatly intensified in emergent man. Schematically, from a scampering, easily frightened monkey-like creature, a stalking, hunting, weapon-making predator emerged with the features of the great carnivore uneasily fused with the characteristics of the easily frightened monkey. The joining together of the carnivore and the herbivore, the stalking predatory killer and the agile monkey escapist, created that heroic coward known as man.

These transformations brought about the evolution of Old Stone Age man. Paleolithic man shows a gradually increasing skill in fashioning tools, weapons, and shelter for himself as well as some belief in an after-life as demonstrated by his burials. The crowning achievement of this pre-human form consisted in the cave art which showed that his brain had acquired the ability to register and recall in detail concrete pictorial images and his hand the capacity for expressing the images within his mind. The magnificent cave art of the late Paleolithic period reveals that man had achieved his full sensory and motor stature.

The art of upper Paleolithic times is dated to around 25,000 to 15,000 years ago. The next stage, which constitutes the final emergence of man, was the evolution of what has been termed the Neolithic period, beginning *circa* 8,000 years ago. Up to this time pre-humans had subsisted by food-gathering and hunting alone. With Neolithic man begins plant and animal domestication, which must be recognized as the first step taken by man in controlling rather than merely exploiting nature. Instead of being at the mercy of the provision offered him spontaneously for his sustenance by the plant and animal world, man began to control his own food supplies, and became able thereby to acquire surpluses, to achieve economic stability, and the leisure and economic sufficiency needed to develop his various cultures and civilizations. As Burkitt states, "The small neolithic communities were doubtless very primitive and simple, but the germ of our own civilization was there. Our own way of life and thought evolved from these early village settlements; it could never have come directly from the cave men of the Old Stone Age."

During the Paleolithic period the mnemonic power and the motor dexterity requisite for man's status were evolved. The transformations that enabled man to achieve what Childe has termed the "Neolithic revolution" may be reconstructed by comparing the mentality needed for hunting and food gathering with that needed for domesticating plants and breeding animals.

The primary reaction of animals to food is to eat and gorge when hungry and to lose all interest in food when sated. With the exception of animals with food-storing instincts, not present in carnivores and the higher primates, the achievement of satiety causes a complete indifference towards food until hunger returns. The carnivore kills and eats only when hungry, and when sated avoids his usual prey. The herbivore consumes food only when hungry and scatters excess when full. These reactions are easily observed in young children and most higher mammals. For plant and animal domestication to arise, an inhibition of this more primary oral reaction must take place in favor of a continued interest in food even amid satiety to the point of retaining excess whether of a plant or animal nature.

To enable the individual to inhibit the primary anorexia that accompanies fullness, it is necessary for the memory of hunger to impinge tonically on consciousness or to be charged with mental energy. Interest in food must be independent of hunger pains or the idea of hunger, and the need for nourishment must rise above and be independent of instinctual pressures. To achieve this, man's consciousness of his needs or self-consciousness must have been enhanced. In addition, for plant domestication the awareness of a causal relationship between the seed and the plant must have arisen to cause the individual to save seeds for planting. This requires the power of reflecting, or bringing the memory of seeds spilt on the earth into connection with the actuality of plants growing out of the earth. The power of reflcting or of forming connections between ideational or pictorial contents is required for establishing a causal relationship.

To achieve the domestication of animals, other shifts in instinctual attitudes must arise. The primary fear-aggression reaction which all animals have to alien species must be inhibited. In the presence of other species, higher animals when they approach or are approached attack or flee, depending upon the size of the animal and the danger involved. Man, being part carnivore, is endowed with the instinct to kill and eat those animals upon which he preys and to flee when not hunting or when faced by larger animals. To domesticate or attach to himself herds and breed animals, particularly larger animals, he must inhibit his more primary reaction of fear and aggression. For if he merely feared he would flee, and his primary aggressiveness would cause him to destroy to the point of depleting his stocks.

The above-mentioned six reactions, i.e., inhibiton of oral drive, the urge to retain excess, inhibition of far and aggression, independence of idea from instinct charge, increased self-consciousness, and increased powers of reflection, form the basis for the transformation from Paleolithic to Neolithic man. Whatever caused these changes is the source of the genesis of

man. The first three shifts in reaction are in accordance with Freud's formulation of instinctual renunciation as the basis of human culture.

In his Apes, Giants and Man, Weidenreich states, ". . . the human brain case attained its greatest evolutionary expansion during the Neanderthal phase and has undergone a distinct diminution since," and the Neanderthal brain "is not more globular than that of modern man but distinctly less so." In other words, the emergence of man was accompanied anatomically by a slight shrinkage in brain volume, an increase in the globularity of the brain, instinctual inhibition, and increased instinctual drive as demonstrated by the heightened aggressiveness in becoming part carnivore and the constant sexual interest. This has been accompanied by a continuation of the evolutionary trend towards increasing fissuration of the brain.

In his origin, man becomes more "brainy" with less brain volume. Instincts increase in intensity and become inhibited. Both the anatomical and behavioral transformations can be explained by the hypothesis that *the genesis of man was achieved by the growth of instinctual drives to the point where they split in two: part retaining their original direction towards the external world and part being turned in against the self.* This splitting in two parallels cell growth and division and the turning of cortical substance into the brain in fissuration. This change would permit increased function with decreased volume, would tend to increase the globularity of the brain, and enable instincts to be increased in intensity as well as more inhibited by being turned against themselves. In addition the turning of consciousness against the self would create the distinctive human characteristics of self-consciousness and reflection.

In his Instincts and Their Vicissitudes, Freud points out the mechanism of turning against the self as one of the four methods of controlling instincts. The other three are reversal into the opposite, repression, and sublimation. From the above considerations turning around upon the subject can be seen to be the primary instinctual change responsible for the transformation of Paleolithic into Neolithic man. Reversal into the opposite, repression, and sublimation are secondary transmutations of instinctual drives which are being blocked by instincts turned inward.

The counter-instinct or instinct turned against the self which is easiest of clinical observation and shows least change in its qualitative aspects as compared with the primary instinct, is self-aggression. In the emergence of man, counter-aggression created a basis for the sense of guilt, from which are derived the other necessary instinctual renunciations. Oral, anal, and aggressive drives become blocked by guilt to produce oral inhibition, the urge to retain, and restraint of the primary fear-aggression reaction toward animals. By establishing a feeling of guilt about destroying and consuming foodstuffs, renunciation of pre-human drives became possible. Thus there arose an instinctual reaction causing man to deny himself, to spare his seeds and stocks, and thus to have them available for future planting and breeding. The cultural monument to this momentous inhibition of instinct is totemism. Animals or plants are exalted and spared or felt guilty about and protected by elaborate fantasies of kinship; a displacement and secondary elaboration upon the creation of guilt about foodstuffs.

In addition, the primary oral drive turned into the self in antithesis to itself to create a second instinctual food-preserving mechanism. The urge to gorge the self with food became inhibited not only by guilt but also by the influence of the oral reaction formation which causes the individual to wish to part with part of what he wishes. By means of the oral reaction formation envy and greed become transformed into altruism and generosity. From this development arises the urge to give up foodstuffs and thus limit oral rapacity. Thereby another instinctual mechanism is provided for preserving seeds for future planting and animals for future breeding. The cultural monument to this instinctual advance is the phenomenon of ritual, tribal, and religious sacrifice.

The anal reaction formation or counter-instinct, which transforms the primary impulse to expel faeces into its opposite of turning excreta into the self, creates the urge to hoard and retain. This provided a third instinctual force in the transformation of an impulsive "eat, drink, and be merry" Paleolithic hunter into a quasi-compulsive Neolithic husbandman or bourgeois who saved part of what he possessed for future planting and breeding. The historical monument to this instinctual transformation, still very active, is the conviction of the capitalist that his hoardings or anal reaction formations are the basis of all culture and civilization.

The primary urge to perceive, i.e., to see, hear, smell, taste, sense, etc. also turned inward into the self to produce the uniquely human characteristic of self-consciousness and reflection. Human intelligence is based on the capacity to register the impressions of the external world (as with lower animals) plus the highly distinctive human power of thinking about the impressions registered or reflecting on them. By this means the phenomena of the external world can be compared and contrasted, ideas or hypotheses as to possible interrelationships can arise which in turn can be proved or disproved by reality testing as previously demonstrated. This is the basis for establishing causal sequences.

Thus the perceptions of seeds and plants would be brought into connection with each other, as seeds are palpably derived from plants. Intelligence (being suffused with antithetical drive) would raise the question whether the opposite occurred, or plants came from seeds. A trial of planting would establish this epochal connection, and plant domestication arose. Thus from perceiving the already perceived arose the power of establishing causal sequences essential for the emergence of Neolithic man. The continued interest in food in the absence of acute hunger pains arose partly from the oral reaction formation which keeps erotisms in a state of continuous interest and partly from the increased self-awareness of all internal processes, including, of course, eating.

A special instance of internalized perception of tremendous value for man's evolution consisted in applying a special set of sounds known as words to all other modalities of experience. The sensory impressions and motor expressions of words act as an inner representation to consciousness of all other types of imagery, granting consciousness a facile means of communicating with experience. An evolutionary trend in this direction is present in mammalian psychology as observed by Maier and Schneirla. They point out: "The transference of responses from the control of one group of sense organs to another is very common. Unlike the lower forms the specificity of reactions to particular forms of stimulation is greatly reduced in mammals." The establishment of language is essentially the transference of image evaluation of all modes of experience into the auditory vocal sphere. An anatomical basis for the domination by the auditory sphere is suggested by Meyer's loop of the visual radiation to the temporal lobe.

A further pre-human step in the direction of language has been revealed by the experiments of Kluver and Bucy. They found that monkeys whose temporal lobes were removed lost their sense of visual discrimination so that they did not know how to respond to previously familiar objects and would mouth them as infants do. In other words, even in lower primates, temporal lobe auditory reactions acquire dominance or act as an interpretive screen between consciousness and the various forms of sense perception.

In man this trend achieves its highest expression through the covering over of all types of sensation by that special type of sensation known as words. All experience becomes represented to consciousness by words, giving rise to language wherein, by means of words, one can recall and express what one has seen or touched, thought or felt yesterday or decades ago. In higher cultures the primary auditory screen of the spoken word becomes secondarily associated with the written (visual) image and with digital skills to create the written word; but this is a secondary development which in the individual and the group must follow after the establishment of the spoken language.

The vast importance of language in the evolution of human intelligence can hardly be overestimated. But it should be realized that language is but another expression of the internalization of primary brain activity that evolved man. In this instance auditory memory and vocal skill turned inward to bring themselves into connection with every possible experience registered in the human mind. By this means consciousness acquired an instrument for contacting what lies beneath, for asking questions of experience, considering the answers given, and testing the answers with other or new experience for the correct answer. A sort of telephone exchange was set up, words being the wires between consciousness and memory. All the past experiences of the individual, and of all other individuals who would communicate, become available to consciousness and the preconscious for dealing with reality.

The turning in on the self of the instincts, responsible for the genesis of man, follows the processes of nervous system development wherein ectoderm specializes into nerve tissue and invaginates into the organism. Language parallels peripheral nerve growth out from the brain and cord to contact tissues and organs. The function of the counter-instincts in inhibiting more primary instincts follows the pattern of neurological development wherein higher centres inhibit lower centres as well as the recently discovered presence of suppressor areas in the cerebral cortex. The counter-instincts are what endow man with his bi-mentality or an unconscious and a conscious, pre-conscious system. This bi-mentality parallels the general biological phenomena of chemical bivalence, central nervous system, and skeletal bi-laterality and bisexuality. Life itself is based on and proliferates equilibria between chemical substances, organ systems, neurological and mental functions.

The above reconstruction of man's genesis explains many of the empirical discoveries of Freud. Thus the phenomenon of ambivalence, so puzzling in its pervasiveness, can be recognized as an essential derivative of the double mentation of man. The counter-cathexis necessary for maintaining repression can easily be seen as derived from the energies firing the counter-instincts. Reaction formation, overcompensations, the tendency towards reversal, the representation by means of the opposite, the storing up and maintenance of psychic tension in more tonic states are also derived from the counter-instincts. The male castration complex, so strange and apparently in contradiction with the basic biological drive of reproduction, can be recognized as the inevitable counter-instinct

to the male's primary genital drive. Penis envy in the woman is the counter-instinct to her vaginal genitality. The peculiar yet profound importance of man's reactions to his anal functions can be better comprehended in terms of the contribution of this zone to the transformation of man's alimentary functions so necessary for food domestication.

In his Totem and Taboo Freud formulates the idea that the murder of the father by the son horde and their subsequent repentance is the origin of totemism, exogamy, guilt, and human culture. Without denying the importance of the son's murderous wishes and probable actions in primeval times in directing his sense of guilt, the above reconstruction of man's genesis would contradict this hypothesis. Man came into existence when the instincts grew sufficiently to split into instinct and counter-instinct. The latter caused the development of guilt, oral and anal reaction formations, the castration complex, and internalized perception, which form the intrapsychic foundations for culture and civilization.

The development of the counter-instincts inhibiting man's more primary impulses or wishes and their associated imagery is the main motive force behind repression and the hiding of the depths of man's nature from his consciousness, creating his "congential idiocy" about mental processes. A historical expression of this evolutionary repression was in the degeneration of man's powers of artistic expression when he entered the Neolithic period of development. With the establishment of the counter-instincts the imagery within his mind and the free manual expression of image and impulse became repressed and distorted, preventing him from achieving the power of artistic expression found in the great cave art.

From the generalized turning of the erotic instincts against the self (the largest component from orality) arises self-love or narcissism. The general importance of guilt and narcissism in the development of the individual and in maintaining each individual as a compliant and submissive member of his society is obvious on a moment's consideration. For guilt punishes the individual for misdeeds in thought or action, and, in combination with narcissism, makes him willing and eager to sacrifice for the group. Men can deny their impulses or obey their societies' dicta only when their guilt can punish them for forbidden acts and their narcissism make them feel noble and righteous for self-denials. Guilt and narcissism are the two tamers of man's primeval instintcs on a historical as well as on an individual basis, causing him to punish himself with self-aggression on doing wrong and causing him to love himself on doing right. Both are palpably and obviously internalized or counter-instincts.

The creation of internalized perception along with the more primary externality perceiving apparatus, endowing man with a double-mindedness, has had somewhat the same influence as combining lenses to develop the microscope and telescope (perhaps projections of this). For as with these instruments of perception, so with the creation of man a new world came into being. By means of his distinctive equipment man has been enabled to create with his mind as well as with his genitalia. The actual processes of mental creativeness, its power to abstract ideas from perception, condense them into concepts, and then reduplicate what has been observed, bear a remarkable resemblance to the germ cell, which also has the power of abstracting and condensing into the minutiae of the gene the structure of the species and can also under favourable circumstances expand into a duplicate of the parent organism.

Thus with the creation of man the life instinct or the forces of biological creativeness moulded an instrument for more perfectly achieving its goals. The death instinct likewise found its highest expression in the genesis of man. Created by a bursting of instinct in two, turned against himself and other selves, endowed with nature's greatest intensity of aggression per individual, and now equipped with monstrous powers of destruction, man is the apotheosis of destruction as well as of creativity.

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GENETIC HOMEOSTASIS [1]

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J. B. S. Haldane recently wrote [2] that "The current instar of the evolutionary theory" may be drawing to its close; although "we are certainly not ready for a new moult, but signs of new organs are perhaps visible." The short book by I. M. Lerner explores some of the "new organs." It is, hence, an important and significant work, which may presage the "new moult"; it may even act as a moulting hormone.

Mendelian populations have been customarily regarded as aggregations of genotypically fairly uniform individuals homozygous for most gene loci, with a scattering of genetically aberrant individuals among masses of "normals." The discovery that many of the "normals" are in fact heterozygous carriers of recessive mutants at first did not appear contradictory to the simple model of the population structure. The mutants, or at least those of them which produce relatively mild physiological or morphological effects when homozygous, could serve as hidden reserves of genetic variability and of raw materials for evolutionary changes. Natural selection usually favors a certain average phenotype in each population; however, the favored phenotype changes hand in hand with alterations of the environment.

It now appears that the above simple model will no longer suffice. Mendelian populations possess remarkable integrative properties; populations are organized supraindividual entities which undergo evolutionary changes as such. According to Lerner, "This change of outlook has caused the integrative properties of populations to assume paramount importance in evolutionary thought, not only for problems dealing with differentiation between populations, but with an even greater force for those relating to genetic phenomena within populations." And again "The laws governing the physiology of populations transcend those governing the physiology of individuals."

The basic facts which require a change of orientation in evolutionary genetics are simple enough. The adaptive norm in many Mendelian populations, at least in those of Drosophila, is made up entirely of complex heterozygotes. Moreover it is the heterozygosity which makes the individual genotypes engender highly adaptive norms of reaction to the environments in which the species normally lives. Homozygotes are usually poorly adapted. The works of Mather and others on Drosophila, and of Lerner and his collaborators on poultry, have disclosed certain peculiar situations which occur when artificial selection forces shifts away from historically established phenotypic and genotypic equilibria in populations. Such shifts imposed by artificial selection are often opposed and counteracted by natural selection. In other words, the genotype of a Mendelian population possesses homeostatic properties which resist sudden change. New homeostatic balance may, of course, be attained by systematic selection, whereupon the change achieved may also become homeostatically buffered.

Normal fitness in outbred Mendelian populations is brought about by most individuals in such populations being heterozygous for numerous gene alleles and gene complexes. Dubinin in Drosophila, and Lerner in poultry, found that inbreeding results in the appearance of, among other things, so-called phenodeviants. These are "heritable complexes and syndromes . . . whose expression could not be ascribed to the action of definite gene-pair differentials. . . . Their appearance is connected with balancing mechanisms in Mendelian populations based on heterozygosis and thus related to the phenomena of inbreeding degeneration." Inbreeding of many stocks of chickens results in the appearance of a certain proportion of individuals with "crooked toes." Inbreeding combined with selection for crooked toes can lead to fixation of this trait, but outcrossing tends to lower its incidence. A very similar situation was described in Drosophila by Dubinin; [3] inbreeding of many quite unrelated strains reveals variable traits called extra vein, veinlet, and network. Dubinin's work was severely criticized by Goldschmidt [4] in an article characteristically entitled "Pricking a Bubble." Lerner reinflates and greatly reinforces this "bubble." More than that, he shows that Dubinin's interpretation fits not only his data but also the observations

[1] Genetic Homeostasis. By I. M. Lerner. John Wiley, New York, 1954: 1–134 p., figs. 1–14. $3.50.

[2] Foreword, by J. B. S. Haldane, to the symposium on "Evolution," No. 7 of the Symposia of the Society for Experimental Biology. 1953.

[3] Experimental investigation of the integration of hereditary systems in processes of evolution of populations. By N. P. Dubinin. Zhurnal Obsch. Biol., **9**: 203–244. 1948.

[4] Pricking a bubble. By R. Goldschmidt. Evolution, **7**: 264–269. 1953.

of Goldschmidt himself and his collaborators,[5] who studied the so-called podoptera effect, which is comparable to the crooked toes in chickens and to the extra veins in Drosophila.

The role of heterozygosity in Mendelian populations appears, then, in a new light. According to Lerner: "Heterozygosity has a dual function in the life of Mendelian populations. On the one hand, it provides a mechanism for maintaining genetic reserves and potential plasticity, and on the other it permits a large proportion of individuals to exhibit combinations of phenotypic properties near the optimum. Underlying both processes is the superior buffering ability of heterozygotes as compared with homozygotes." And: "It is heterozygosity per se rather than the genic contents of the individual which is the important consideration." Lerner is fully aware that this view represents a partial return to the "pre-Mendelian notions about the effects of inbreeding." But this return is forced on us by the rapidly accumulating evidence that developmental homeostasis (referred to also as canalization) is a characteristic chiefly of heterozygotes. To be sure, the new theory is not free of difficulties; the existence of self-fertilizing species shows that some homozygous genotypes do possess high adaptive values. It follows that "The particular level of obligate heterozygosity for each species and probably for each less inclusive Mendelian population is determined by its evolutionary history." Much work will, however, be necessary to explore all the implications of this view.

The importance of the phenomena discussed by Lerner for practical breeding, as well as for the evolution theory, is obviously considerable. Breeders cannot take it for granted that the average performance of a population can easily be made equal to that of the maximum performance of individuals in that population. Evolutionists will have to revise their ideas about the nature of changes in the population genotypes which lead to adaptive evolution. Lerner refrains from considering the bearing of the new conceptions of population structure on the welfare of human populations. This is a matter which cannot be treated lightly, but it requires serious thought. The book is so short that it becomes of necessity one long argument, very closely reasoned, but presented with that degree of clarity which is attainable only through a complete mastery of the subject.

[5] The podoptera effect in Drosophila melanogaster. By R. Goldschmidt, Aloha Hannah, and L. R. Piternick. Univ. California Publ. Zool., **55**: 67–294. 1951.

ANIMAL CYTOLOGY AND EVOLUTION [1]

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The first edition of White's work (1945) was among the small number (about eight) of books which brought about, since 1940, a far-reaching synthesis of the contributions of various biological disciplines in the light of the evolutionary idea. It is fair to say that the modern "synthetic" theory of evolution has taken shape to a considerable extent in these books. A new edition of White's book has become necessary nine years after the first; this is evidence of the rapid progress of evolutionary biology in general and of cytogenetics in particular.

Though the plan of the book has remained essentially unchanged from the first edition, the text has been extensively revised and in many places rewritten entirely. The book contains an account of the chromosome structure and chemistry, of meiosis, chromosomal changes (mutations) and their occurrence in natural populations, chromosomal polymorphism, chromosomal evolution on the race, species, and higher levels, and of mechanisms of sex determination and parthenogenesis. A tremendous amount of information is ably summarized in every chapter. The first edition had a bibliography of 37 pages, the new one has 53 pages, with about 28 references per page. Professor White is fair, judicious, and patient in his evaluations of this mass of evidence, uncertain and contradictory though some of the latter may be. And yet White's presentation has not crumbled into a jumble of disconnected data and references; the exposition is masterful, with basic principles standing out clearly, bolstered rather than smothered by the accumulation of the often equivocal data. This book is not merely a valuable guide to scattered literature but an analysis of fundamentals.

As in the first edition, White has been able to keep a balance between a preoccupation with the unusual, aberrant, and overspecialized on

[1] Animal Cytology and Evolution. By M. J. D. White. Cambridge University, University Press, Cambridge, 1954: I–XIV, 1–454, figs. 1–147. $8.50.

the one hand, and a disregard of the empirically observed diversity of cytological mechanisms on the other. Such overvaluation and underestimation of the existing variety of cellular processes have often stultified whole chapters of cytology. Those familiar, as well as those unfamiliar, with the first edition will find the second edition an indispensable guide and manual.

Note added in proof. White's book has been harshly, and unjustly, criticized in a review by C. D. Darlington (Nature, vol. 175, pp. 4–5, January 1, 1955). Darlington objects that White has disallowed some of the speculations which Darlington had put forward: "He [White] writes, therefore, not of evolution as we [Darlington] understand it, but of comparative anatomy." Yet, the first edition of White's book has been, and the second probably will be, criticized by others because White is not content merely to register cytological observations but seeks to understand them in the light of their evolutionary origins and significance. These diametrically opposed criticisms put in bold relief the difficulties with which White had to struggle to achieve the balanced synthesis which he has achieved. On the one side, he had to contend with the tendency of some cytologists to consider only the facts which happen to fit in the straitjacket of a particular theoretical scheme. On the other side, he had to deal with the deficient understanding of the scientific method in those who would make cytology an archive of descriptions of more or less meaningless microscopic pictures. Now, the tendency of some cytologists to draw no distinction between observed facts and their theoretical interpretations conveys a false impression that all problems of cytology have been solved. This retards further discovery. And after all, there is a difference between science and science fiction. On the other hand, a disinclination to distinguish between the general and the special, the meaningful and the accidental, the functional and the irrelevant, stultifies knowledge. It should be realized that cytological structures and processes exist because they fulfill certain biological needs, and that the investigator should try to find out what these needs are. White's achievement is that he is able to reach a proper balance between these opposing errors.

ATLAS OF MEN [1]

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The lack of agreement about the classification of human races is notorious. Things stand scarcely better with intra-populational variability. Attempts to describe and classify variations in the human physique have been made ever since Hippocrates. Not very long ago it was proposed to distinguish three constitutional types: digestive or pyknic, muscular or athletic, and leptosome or asthenic. The proposal broke down since it involved typological thinking at its worst; the "types" are extreme variants, and a great majority of people have to be described as intermediates between or mixtures of the three arbitrary "types." Professor Sheldon has set forth a method of description of human physique in terms of three "components"—endomorphy, mesomorphy, and ectomorphy—which are assumed to characterize the relative development of the endodermal (digestive), mesodermal (muscular and skeletal), and ectodermal structures. The "components" are rated by visual estimation, and expressed in a quasi-quantitative fashion by assigning values from 1 (minimal) to 7 (maximal). Only 88 of the possible permutations of the component ratings have been found among the 46,000 male subjects studied. Each of the 88 "somatotypes" is described by three numerals, such as 3 5 2, which stand for the ratings of the endo-, meso-, and ectomorphic components, respectively.

Since its first publication in 1940, Sheldon's method of somatotyping has gained enthusiastic followers as well as relentless opponents, and has become one of the controversial issues in anthropolgy and human biology. Most critics challenge the biological validity of the "components," and especially the reliability of their rating by inspection of the somatotype photographs, representing the front, lateral and rear views of the person taken in the nude. Obviously the bodily form changes inexorably with age; and surely it is modified by nutritional states, health or disease, and mode of life. Could the permanent constitutional parameters, which the somatotype is claimed to represent,

[1] **Atlas of Men.** By William H. Sheldon, with the collaboration of C. Wesley Dupertuis and Eugene McDermott. Harper & Bros., New York, 1954: I–XVI, 1–357 p., 1175 photographs, 19 tables. $10.00.

be discerned despite all the changes and modifications? Sheldon and his followers maintain that this can be done by trained and experienced observers; the critics are not convinced. The Atlas of Men contains the somatotype photographs of 1,175 male subjects, each taken in the three standard aspects. These 1,175 men have been chosen among 46,000 examined to illustrate the 88 somatotypes as they appear in individuals of different ages. Assuredly the publication of this enormous work will not end the controversy. What it accomplishes, however, is showing just what bodily shapes Sheldon includes in each of his somatotypes. The somatotypes are, then, no longer "something in Sheldon's head"; they can be seen in the photographs. This does not necessarily validate the technique of somatotyping; it does make this technique more communicable. To those interested in human morphology or in human evolution, the Atlas has a permanent and unconditional value of documentary evidence.

Geneticists and evolutionists may well be pleased to find that two of their basic concepts, those of the genotype and the phenotype, are from time to time rediscovered by colleagues working in other disciplines. Sheldon defines the somatotype "as a trajectory or pathway through which the living organism will travel under standard conditions of nutrition and in the absence of grossly disturbing pathology." Now the "trajectory" of the human bodily form is obviously a succession of phenotypic states ("presentations" according to Sheldon) which an individual displays during his lifetime. The phenotype is constantly changing and has "no continuance in time." The succession of the phenotypes is determined by the genotype ("morphogenotype") and by the sum total of the environments through which the individual passes, in other words, by the individual's biography. Two alternative formulations might then be considered, each useful for dealing with particular problems. A geneticist speaks of the norm of reaction displayed by a given genotype in all possible environments. This includes the "normal" and the "abnormal," natural and artificial, healthy and pathological, morphological and physiological, macroscopic and microscopic. To Sheldon, a narrower concept is operationally preferable. The somatotype is that part of the norm of reaction expressed in the bodily form, and restricted to the framework of only those environments which are considered not "grossly disturbing." But even so, for Sheldon the somatotype is by definition permanent to the same degree to which the genotype is permanent. The manifestation of the somatotype can and does change; the somatotype does not. Whether this constant can be observed and evaluated with the aid of a given technique is quite another matter. But to speak of changes in an individual's somatotype is sheer confusion.

In addition to the photographs, the Atlas gives for every somatotype a table of weights for ages 18 to 63 years and for heights from 61 to 75 inches, as well as a curve for the age changes in the ratios of height divided by the cube root of weight. These data might be very useful for making the criteria of somatotyping more explicit and communicable. Unfortunately, no information is given concerning the numbers of observations on which each of the points entered on the curves is based, nor concerning the variability observed for any of the ages. This leaves in the dark the important question of the degree of reliability of the values that are reported. This matter is even more acute in the case of the "weight for height and age" figures; in the absence of a statement to the contrary we must assume that these figures are to an unknown degree extrapolations and interpolations from the relatively few actually observed points, which are not identified as such. The validity of tables of this sort may well be questioned, and one can only hope that Sheldon will publish the necessary data to permit a critical evaluation of the information that is available.

According to Sheldon, the somatotype manifests itself not only in the bodily form but on the behavioral and personality levels as well. The Atlas, therefore, contains brief characteristics of "some of our present impressions and speculations regarding dietary, behavior and clinical tendencies which may be associated with the constitutional patterns expressed in the somatotypes." Some of these characteristics are amusing reading. Thus the reviewer finds that his somatotype (which happens to be 3 5 2 with a trace of "academic displasia") "may carry the load into old age, perhaps along with such miscellaneous other insults as heavy use of toxic drugs like tobacco and alcohol, irregular life habits and so on. . . . To watch a 3 5 2 is to relax a little, even though he is heavily muscled and if aroused might kick your ribs in." This is at any rate better than to be a 3 3 4, the "rather unremarkable, moderately frail little fellows who seem never to be very well fed, or well loved, or even much attended to." Professor Sheldon is definitely unfair to endomorphs like 5 5 1 or 6 3 1, who rarely go to college but often ride on New York subways, and suggest to him balloon tires and soft cushioning.

The idea that personality may be correlated with physique, and both personality and physique may be jointly conditioned by the genotype, is often disallowed with some hostility. The hostility is a result of a misunderstanding of the nature of heredity which continues to be widespread even among biologists, not to speak of

non-biologists. Personality is not inherited as such, because sex cells, which transmit heredity, have no personality; what is inherited is a norm of reaction to the environment which may bring about, among other things, different personality traits in different environments. People may be "well loved," and "much attended to" regardless of their somatotype; nobody's heredity guarantees being loved or, for that matter, being hated. But one can hardly doubt that, in our culture, a physique which is regarded as handsome may mould the personality of its possessor in ways different from a physique which is not considered so comely. A physique which brings about bodily strength or agility is likely to favor in its possessor personality traits different from those which a softer physique may induce. In this simple sense, some correlations of personality with physique are bound to exist, and the observed variance in personality and in physique will in all probability have a genetic component. On the other hand, one must beware of the old fallacy of assuming that people of a given body build are bound to behave in certain ways regardless of circumstances.

The basic fact to be kept in mind in any consideration of variability in human populations is that every individual has a unique and nonrecurrent genetic endowment, and hence a unique "constitution." Discernible constitutional types or somatotypes can, under a Mendelian system of heredity, exist only if a relatively small number of genes with relatively large phenotypic effects are represented in the gene pool by frequencies not too close to zero or to unity. In other words, the existence of two or more biologically valid and clearly distinguishable constitutional types within a population means that this population is polymorphic for body build. The fundamental question which constitutional research will have to answer is whether the somatotypes do or do not correspond to some genetic polymorphism. This question is not touched in Sheldon's work but the Atlas will be useful, or even indispensable, in any investigation that may be undertaken.

Those who do not like light humor mixed with weighty scientific exposition may find it frivolous assigning to each somatotype an animal "totem" with an accompanying racy characteristic. Thus, the somatotype 3 5 2 has for its totems "Little horses, ponies, burros. Sturdy, sure-footed hayburners, built close to the ground, more for security than for speed, and dependable in rough country." Other totems are as diverse as wasps, falcons, small and big cats, various breeds of dogs, elephants living and fossil, bulls, kangaroos, under-the-barn kitties, anteaters, sperm whales, etc. In places it appears that the author takes his own joke more seriously than he intended.

The Atlas of Men is a stimulating book because it raises many more interesting and important questions than it answers. This is a book with a future.

PHILLIPINE AMPHIBIA [1]

RALPH G. JOHNSON

The Phillipine Zoological Expedition, 1946–1947, of the Chicago Natural History Museum presented the opportunity for a much needed review of the Phillipine Amphibia. Two aspects of Inger's contribution should be of general interest to the readers of EVOLUTION. This is the first major work in which the ecological-morphological concept of a taxon has been consistently applied to an extensive fauna. Further, the zoogeographic considerations illuminate the general problem of the faunal affinities of the Phillipine Islands.

The notion that the genus can be a more meaningful taxon when it exhibits ecological as well as morphological integrity, is not a novel one. The application of such a philosophically satisfying principle to the practical systematics of a major fauna is, however, worthy of note. Inger attempts to define the genus as being "characterized by an assemblage of morphological features contributing to an adaptive pattern that can be shown to have a fundamental ecological significance." By paying more than lip service to the ecological implications of morphology, he aims at a classification which will more faithfully reflect adaptation and, hence, evolution.

A particularly illuminating example of the application of this principle concerns his disposition of the genus *Hylarana*. This group is distinguished from the genus *Rana*, to which it is intimately related, by the presence of a circummarginal groove around the end of the digit. This morphological distinction is not accompanied by an ecological shift away from the *Rana* way of life. In contrast is the relationship between *Rana* and *Cornufer*. *Cornufer* is a group of species in which the webbing of the

[1] Inger, R. F., 1954. Systematics and zoogeography of Phillipine Amphibia. Fieldiana, 33 (4) : 183–531. Pub. No. 732. 70 figs. $6.00.

foot is greatly reduced or absent. The outer metatarsals of this species are bound together for nearly their entire lengths. This morphological condition corresponds to a shift into a different ecological sub-zone with respect to *Rana*. The fully webbed *Rana* is predominantly aquatic while *Cornufer* is typically an inhabitant of the forest floor. *Cornufer* is recognized by Inger as a genus while *Hylarana* is not. He regards the morphological difference between *Cornufer* and *Rana* as directly associated with an ecological shift of greater significance than any seen between *Rana* and *Hylarana*.

This ecological approach to the genus is not calculated to make the practical work of the taxonomist any easier. The recognition of a genus in these terms will call for more than morphological data. It will have the disturbing effect of forcing more taxonomists out of doors. But if our systematics is going to mean more than arranging postage stamps in a catalogue then the effort is worth the gain in understanding.

In a detailed zoogeographic analysis, Inger persuasively demonstrates that the Phillipine Amphibia are predominantly Oriental in derivation. Of the fifty-six Phillipine species recognized in his report, forty-three can be shown to be non-endemic western species or endemic species of western affinity. This will come of no surprise to Ernst Mayer with respect to his studies of the islands but should cause some concern among the Dickerson school of Phillipine zoogeographers. Also of interest, in this report, is Inger's review and evaluation of the possible modes of dispersal of amphibians through sea islands.

Only as our knowledge of the Phillipine fauna increases, can we properly gauge the success of Inger's treatment. However, whether his systematics hold up or not, he has succeeded in presenting a faunal report more succulent than the traditional arid catalogues of form.

CORRIGENDA

The following correction of a statement in a footnote of EVOLUTION, **8**: 176 (1954), Experimental Studies of Gene Frequencies in Very Small Populations of *Drosophila melanogaster*: I. Forked, has been received from Professor Sewall Wright, co-author with Dr. Warwick E. Kerr:

The percentage of fixation of the mutant gene, at equilibrium in the form of the distribution of gene frequencies, in the theoretical case of irreversible mutation in populations of 3 monoecious individuals, with random gametes, is 4.34 per cent (instead of 4.53 per cent) and that for fixation of the type gene (balanced by mutation) is 16.31 per cent (instead of 17.05 per cent) both in terms of the unfixed populations of the *parental* generation. The figures given were for the distribution of population types, including newly fixed populations, in terms of the total of unfixed populations in the *offspring* generation.